Bull. Southern California Acad. Sci.
121(1), 2022, pp. 1–26
© Southern California Academy of Sciences, 2022

Differences in Trophic and Community Structure of Kelp Forest Fishes Inside and Outside of Three Long-standing MPAs in the Southern California Bight

Parker H. House and Larry G. Allen

Department of Biology, California State University Northridge, Northridge CA 91330-8303

Abstract.—In many marine ecosystems worldwide, overfishing is a prominent cause in removing large predatory fishes from ecological communities. Fluctuation in the abundance of higher trophic level species can transform an ecosystem's structure and function by altering trophic interactions through density-mediated top-down control. Accordingly, understanding the extent to which humans indirectly influence a community through altering predator abundance is of critical importance. Thus, during the summer of 2013 and 2014 the impacts of fishing on the trophic structure of kelp forest fishes were examined within the Southern California Bight. In 2013, we tested whether decreased abundance through fishing for higher trophic level predators relieves predation pressure on lower trophic level prey. Using a combination of underwater survey techniques, density (no. fish/100 m^2) and biomass (g/100 m^2) of conspicuous fish species were sampled inside and outside of three long-standing Marine Protected Areas (MPAs) off La Jolla, Santa Catalina Island, and Anacapa Island, California. We found that the secondary carnivore and herbivore/omnivore trophic levels were significantly lower in density and biomass outside of MPAs. Inversely, the primary carnivore trophic level biomass was higher outside of MPAs. At the species level, we observed a lower abundance outside MPAs of large kelp bass (>25 cm) and higher densities of potential prey, kelp perch. Other primary carnivore fishes (blacksmith and señorita) showed a non-significant trend of higher biomass outside MPAs. Our results provide evidence of trophic level changes due to fishing pressure and provide support for a possible weakening of top-down control on specifically the kelp perch population through the removal of large kelp bass outside MPAs. The removal or recovery of predators can greatly influence an ecosystem. As more recent studies suggest that indirect community effects of fishing and protection can take up to decades to detect, it is necessary to document the continued changes on the structure, function, and dynamics of the kelp forests and rocky reefs off southern California.

In marine ecosystems, fishing is the most exploitative anthropogenic influence on the abundance, biomass, and diversity of organisms within these communities (Jackson et al. 2001; Aburto-Oropeza et al. 2011; Zellmer et al. 2018). Intense fishing pressure has directly affected the abundance, size structure, and genetic diversity of targeted fished populations (Pauly et al. 1998; Bianchi et al. 2000; Hauser et al. 2002). Many of these target species are large-bodied, higher trophic level fishes (Myers and Worm 2003). Direct removals of these large predators can indirectly increase prey abundance and shift the consumer dominance to lower trophic levels (Baum and Worm 2009). An example of higher trophic level species releasing predation pressure on prey abundance was documented after the collapse of the

Downloaded from http://meridian.allenpress.com/scasbulletin/article-pdf/121/1/1/3078263/i2162-4534-121-1-1.pdf by guest on 23 December 2024

cod fishery off Newfoundland in 1992, which led to the outbreak in the population abundance of dogfish, skates, shrimp, sea urchins, and lobster (Worm and Myers 2003; Steneck et al. 2004; Frank et al. 2005). However, indirect effects of fishing on an ecosystem are not exclusive to large commercial fisheries or more depauperate temperate regions.

An increasingly common way to combat the effects of overfishing has been the implementation of 'no-take' marine protected areas (MPAs). Due to the protracted influence by humans on nearshore marine communities, MPAs may serve as the best available means to test the ecosystem effects of fishing (Tegner and Dayton 2000). Past studies and global syntheses have shown that MPAs greatly increase the biomass and numerical densities of targeted fish populations (Halpern 2003; Barrett et al. 2007; Froeschke et al. 2006; Tetreault and Ambrose 2007; Hamilton et al. 2010; Lester et al. 2009; Caselle et al. 2015; Jaco and Steele 2020). In temperate systems, mean biomass for these species inside reserves can increase as much as 554% (Lester et al. 2009) compared to nearby fished locations.

Of the kelp forest fishes off southern California, the two most abundant predators targeted by fishing are the California sheephead (*Bodianus pulcher*) and kelp bass (*Paralabrax clathratus*). Both species have been shown to respond well to protection by increasing in density, size, and biomass inside MPAs throughout the Southern California Bight (Froeschke et al. 2006; Tetreault and Ambrose 2007; Hamilton et al. 2010; Jaco and Steele 2020). Sheephead abundance can regulate the size of red sea urchin populations (Cowen 1983; Hamilton and Caselle 2015; Seldon et al. 2017) and black sea urchin behavior (Nelson and Vance 1979). Furthermore, the decrease of sheephead biomass due to fishing outside MPAs has indirectly alleviated predation pressure on strongylocentrotid urchins, and through cascading effects, suppresses kelp abundance (Babcock et al. 2010). Unlike the specialist invertivore, sheephead, kelp bass is the predominant generalist piscivore on rocky reef kelp forests off southern California, and are the most important predator of reef fishes off Santa Catalina Island (Carr 1991; Steele 1997a; 1997b; Steele et al. 1998) and likely throughout the Southern California Bight. Therefore, large kelp bass have the potential to regulate lower trophic level fishes.

Kelp bass are one of the most important species in southern California recreational marine fisheries (Allen and Hovey 2001; Jarvis et al. 2004), and their overall biomass has decreased by 90% since the 1980's (Erisman et al. 2011). However, protection via MPAs appears to be beneficial, as orders of magnitude higher kelp bass biomass have been reported inside compared to outside protected areas (Froeschke et al. 2006; Tetreault and Ambrose 2007; Hamilton et al. 2010). Kelp bass are known to decrease population sizes of conspicuous (Schmitt and Holbrook 1985; Anderson 2001) and cryptic prey reef fishes (Steele 1997a; 1997b; Steele et al. 1998; Steele 1999). They are crepuscular ambush feeders of a wide variety of both benthic and water column prey (Hobson and Chess 2001). Smaller fish feed on zooplankton and macroinvertebrates. However, large individuals >400 mm SL feed nearly exclusively on fishes, many of which are reef-associated perciformes (Quast 1968a). Prey fishes include giant kelpfish, señorita, blacksmith, kelp perch, shiner perch, young rockfish, cryptic species such as cottids and gobiids, and transient pelagic fishes including clupeiforms and topsmelt (Quast 1968b; Steele 1997a; 1997b; Steele et al. 1998; Anderson 2001; Hobson and Chess 2001). However, changes in prey fish population sizes have not been observed due to decreases in kelp bass abundance via fishing off southern California.

Several studies have investigated differences in abundance of target and non-target kelp forest fish species off southern California. Hamilton et al. (2010) and Caselle et al. (2015) researched the changes in species and functional trophic groups in relation to protection

Downloaded from http://meridian.allenpress.com/scasbulletin/article-pdf/121/1/1/3078263/i2162-4534-121-1-1.pdf by guest on 23 December 2024

Table 1. Adult kelp forest/rocky reef conspicuous fishes observed during surveys. Species described by water column position (Holdfast, Midwater, and Canopy) and appropriate adult trophic level above primary producers: HO = Herbivore/Omnivore; PC = Primary Carnivore; SC = Secondary Carnivore. Compiled from Cross and Allen (1993), and Horn and Ferry (2006).

Scientific name	Common name	Canopy	Mid	Holdfast	Trophic level
Brachyistius frenatus	kelp perch	x	x		PC
Cymatogaster aggregata	shiner perch	x	x		PC
Embiotoca jacksoni	black perch			x	PC
Embiotoca lateralis	striped seaperch			x	PC
Rhacochilus toxotes	rubberlip seaperch	x	x	x	SC
Phanerodon vacca	pile perch			x	SC
Girella nigricans	opaleye	x	x	x	HO
Kyphosus azureus	zebraperch	x	x	x	HO
Medialuna californiensis	halfmoon	x	x	x	HO
Oxyjulis californica	señorita	x	x	x	PC
Halichoeres semicinctus	rock wrasse			x	PC
Bodianus pulcher	California sheephead		x	x	SC
Chromis punctipinnis	blacksmith	x	x	x	PC
Hypsypops rubicundus	garibaldi			x	PC
Sebastes atrovirens	kelp rockfish	x	x	x	SC
Sebastes serranoides	olive rockfish	x	x	x	SC
Sebastes serriceps	treefish			x	SC
Paralabrax clathratus	kelp bass	x	x	x	SC
Paralabrax nebulifer	barred sand bass			x	SC

and biogeographic differences throughout the northern Channel Islands marine reserve network five- and ten-years post establishment. Upon which after ten years of protection, targeted fish species increased in biomass by 27%. A spillover effect was not observed five years post establishment of the Channel Islands marine reserve network. Also, Tetreault and Ambrose (2007) analyzed target and non-target species of the kelp forest fish community inside and outside of long-standing MPAs encompassing the entire Southern California Bight. However, this data was from underwater benthic surveys conducted over 20 years ago (1997-1998). Both studies found decreases in target secondary carnivores (kelp bass and sheephead), but no indirect effects on non-target lower trophic level fishes. However, recently two studies (Yates et al. 2020; Eisaguirre et al. 2021) concluded that marine reserves can have direct and indirect effects on predators and their prey. Yates et al. (2020) further suggested that their results emphasize the importance of accounting for site-specific differences in food web structure before applying ecosystem-based metrics to fishery management. Conspicuous kelp forest fishes that were observed during the present study have a variety of feeding habits that allow them to be grouped into specific functional trophic levels and occur in different vertical regions of the kelp forest (Table 1).

Although indirect effects of fishing on the kelp forest fish community have only recently been observed off southern California, this community is changing. After the Proposition 132 gill net ban in 1994, the endangered apex tertiary carnivore, giant sea bass (*Stereolepis gigas*), has shown signs of a return and gradual increase to the southern California kelp forest ecosystem since the population collapse due to overfishing (Pondella and Allen 2008). Giant sea bass feed on a wide variety of larger fish species, including the heavily fished kelp bass (Domeier 2001; Love 2011; Erisman et al. 2011). The growing emergence of this top predator can further influence ecosystem dynamics off southern California with the

Downloaded from http://meridian.allenpress.com/scasbulletin/article-pdf/121/1/1/3078263/i2162-4534-121-1-1.pdf by guest on 23 December 2024

potential to exacerbate the effects of fishing and trophic relationships within the kelp forest community. The possible return of giant sea bass, coupled with growing evidence that indirect effects of fishing on marine communities can take decades to detect (Daan et al. 2005; Babcock et al. 2010; Estes et al. 2011), warrants investigation into fish community dynamics off southern California. We evaluated how fishing pressure may directly and indirectly influence the trophic structure of kelp forest fishes off southern California.

To address this question, we used a combination of survey methods to assess biomass and numerical densities of kelp forest fish trophic levels and community assemblage at the species level. We surveyed three sites containing over 25-year-old MPAs as a control for nearby locations subject to fishing pressure throughout a wide geographic range (235 km) within the Southern California Bight. The objective of this study was to determine whether a direct decrease through fishing of higher trophic level predators indirectly releases predation pressure on lower trophic level prey species within the fish community. With fish numerical and biomass densities as response variables, we tested the hypotheses that 1) the secondary carnivore trophic level will have a lower abundance outside of MPAs; 2) the primary carnivore level will have a higher abundance, while the herbivore/omnivore level will not significantly change outside of MPAs; and 3) lower abundance of large >25 cm piscivorous kelp bass correlates with a higher abundance in prey species outside MPAs.

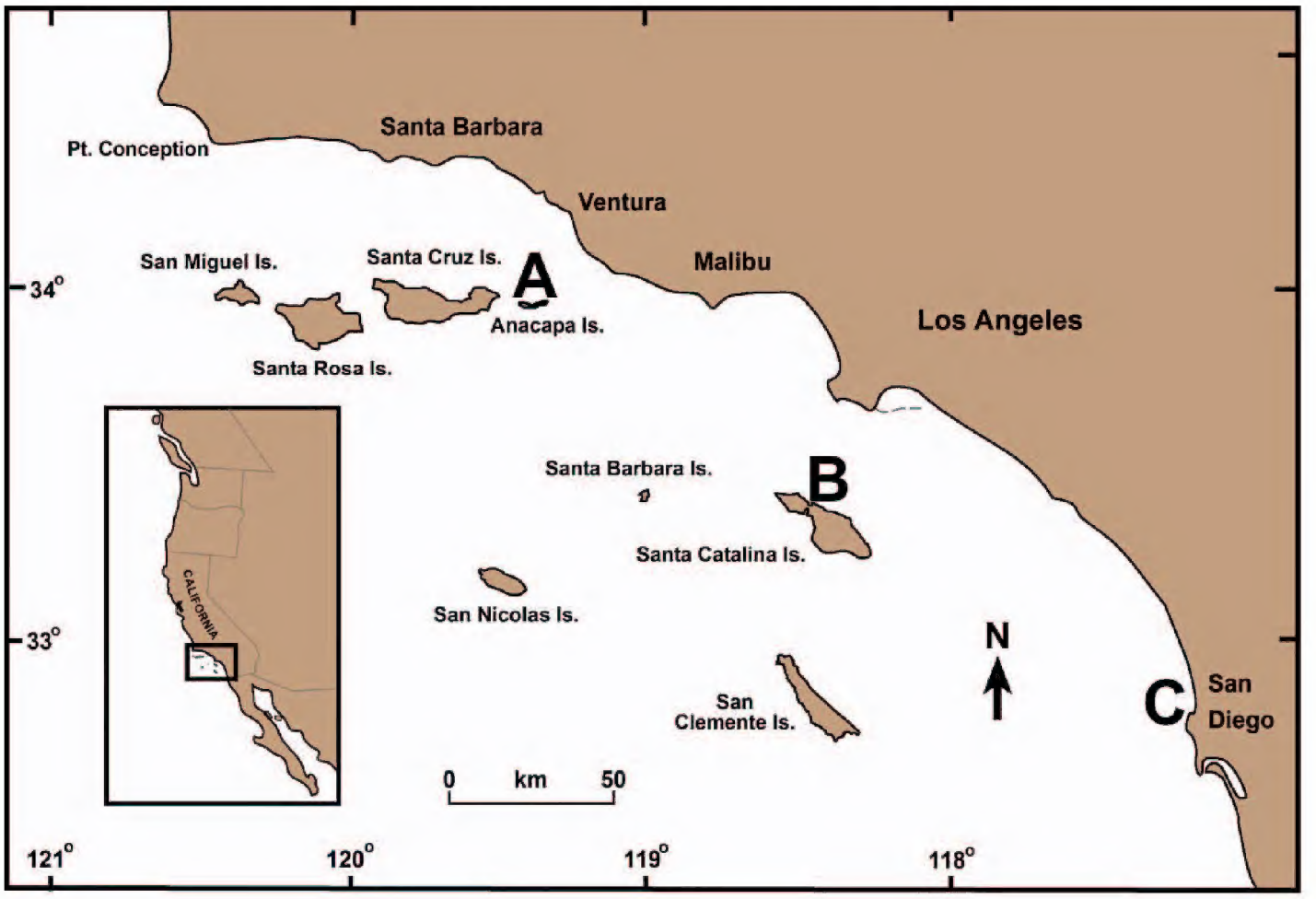
Materials and Methods

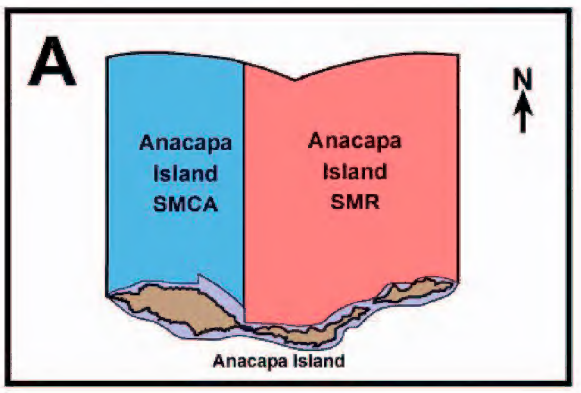
We surveyed kelp forest fishes at three sites off southern California containing the oldest MPAs within the Southern California Bight and nearby unprotected areas of comparable habitat where fishing was permitted (non-MPAs). This design was implemented to investigate the effects of fishing on the kelp forest fish community. Sites were located off La Jolla, Santa Catalina Island, and Anacapa Island, CA (Fig. 1). Sampling was conducted from June 6 to August 9, 2013.

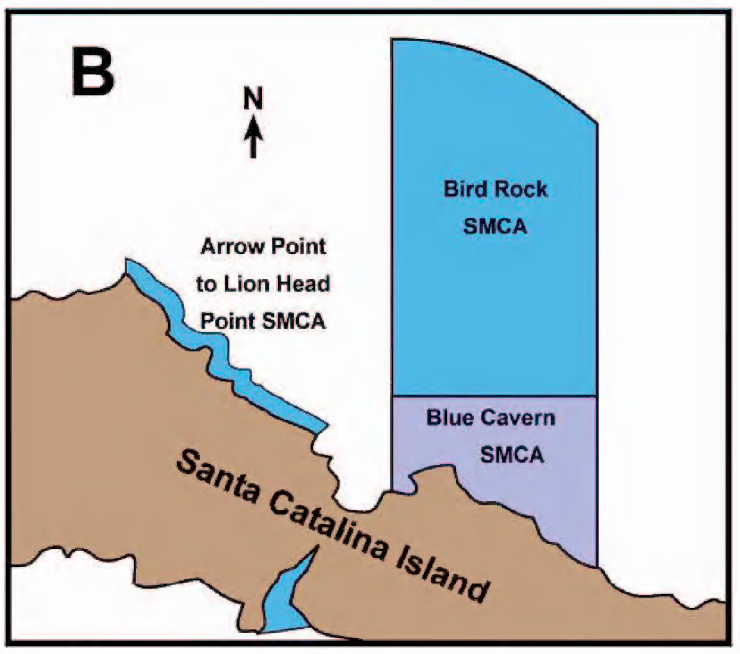
The MPA located off Point La Jolla is the Matlahuayl State Marine Reserve (SMR). Boundaries of the Matlahuayl SMR to the coastline are located at 32° 51.964′ N, 117° 15.233′ W; 32° 51.964′ N, 117° 16.400′; and 32° 51.067′ N, 117° 16.400′ W. The Matlahuayl SMR (Fig. 1) was originally established as the San Diego-La Jolla Ecological Reserve in 1971 and prohibits take of all living resources. Transects in non-MPA locations (32° 51′ 10.40″ N, 117° 16′ 45.57″ W) were conducted off Boomer Beach in areas containing similar substrate composition of red algal turf reefs, relief 1-3 m high, and comparable *Macrocystis* density to the Matlahuayl SMR (Parnell et al. 2006). Fishing effort at Point La Jolla is likely focused on the line of the MPA, as is shown in California Department of Fish and Wildlife commercial passenger fishing vessel (CPFV) catch per unit effort (CPUE) maps, and was observed (including spearfishing and private fishing boats) during this study. Transects in the non-MPA were at least 0.5 km west from the Matlahuayl SMR boundary.

Santa Catalina Island is located 35 km southwest of Los Angeles. The MPA off the southeastern side of the isthmus (Fig. 1) is the no-take Blue Cavern Onshore State Marine Conservation Area (SMCA). This MPA has expanded from the original boundary at Chalk Cliffs to Yellowtail Point as a part of the Marine Life Protection Act (MLPA). The MLPA was implemented in southern California in January 2012 to reevaluate existing and design new MPAs. Surveys for this study were only done in the original Catalina Marine Science Center State Marine Reserve established in 1988, encompassing an area of ~0.21 km^2. Surveys within this MPA were located from the USC Wrigley Institute's intake

Downloaded from http://meridian.allenpress.com/scasbulletin/article-pdf/121/1/1/3078263/i2162-4534-121-1-1.pdf by guest on 23 December 2024







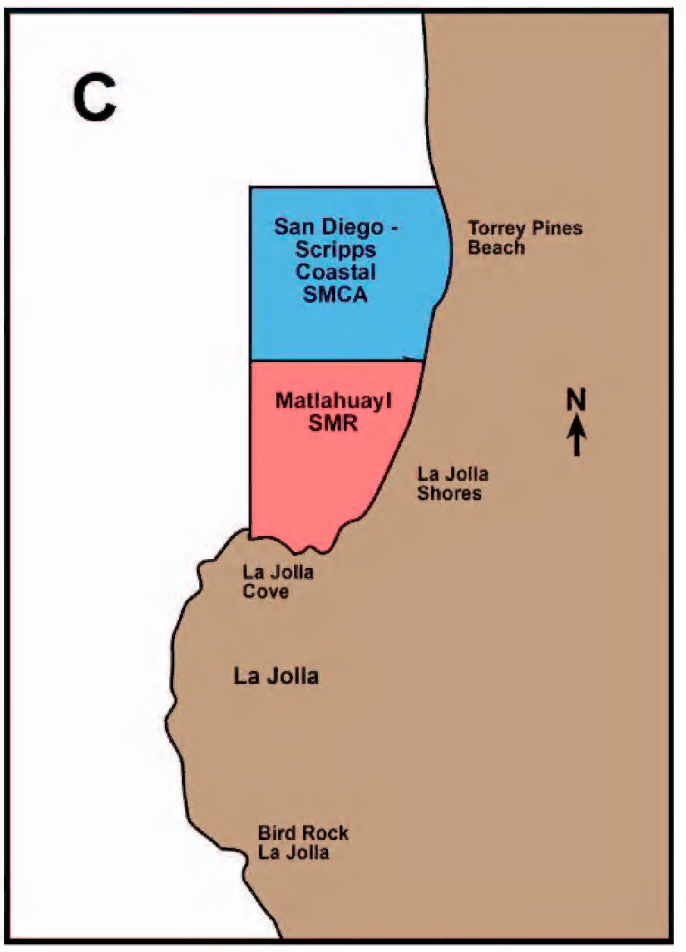


Fig. 1. Map of study sites within the Southern California Bight. A = Anacapa Island, B = Santa Catalina Island, C = La Jolla. Non-MPA locations were located west-southwest of Matlahuayl SMR, within the Arrow Point to Lion Head Point SMCA, and the leeward side of Anacapa Island.

Downloaded from http://meridian.allenpress.com/scasbulletin/article-pdf/121/1/1/3078263/i2162-4534-121-1-1.pdf by guest on 23 December 2024

pipes (33° 26′ 47.50″ N, 118° 29′ 09.89″ W) to the Pumpernickle Cove mooring (33° 26′ 53.79″ N, 118° 28′ 45.64″ W) and east of Pumpernickle (33° 26′ 56.70″ N, 118° 28′ 33.63″ W). Non-MPA surveys were conducted off Lion Head (33° 27′ 12.08″ N, 118° 30′ 04.62″ W), Sphinx Rock (33° 27′ 20.08″ N, 118° 30′ 29.48″ W), Eel Cove (33° 27′ 21.34″N, 118° 30′ 38.33″ W), Little Geiger (33° 27′ 27.07″ N, 118° 30′ 51.39″ W), and Howland's Landing (33° 27′ 31.32″ N, 118° 30′ 57.97″ W). This area is a part of the Arrow Point to Lion Head SMCA. However, only take of invertebrates is prohibited within this SMCA and it served as the non-MPA location for fish surveys. Non-MPA locations were 1.6 km from the MPA boundary.

Anacapa Island is a part of the Channel Islands National Park and is 18 km off the coast of Port Hueneme, California (Fig. 1). On the north side of the island lie the Anacapa SMR and the Anacapa SMCA. The Anacapa SMR was originally established as the Anacapa Island Ecological Reserve in 1978. Boundaries of the Anacapa SMR encompass the east and west islets. This MPA prohibits take of all living resources and has an area of 29.9 km^2. Likewise, the Anacapa SMCA was originally a part of the Anacapa Island Ecological Reserve with seasonal openings to fishing. As of 2003, this MPA was designated as a no-take of living, geological, or cultural resources except for the recreational take of spiny lobster and pelagic finfish. Pelagic finfish are transient species to the rock reef/kelp forest system and use a wide range of habitats. The SMCA was protected against fishing for at least ten years, therefore, the Anacapa SMCA was treated as a part of the MPA region surveyed at this site. The waters off the northern side of Anacapa Island are protected from fishing. Although potential oceanographic differences in currents and wave exposure could be present, the best available reference location for non-MPA surveys was located off the southern side of the island, where habitat conditions were similar to those of the northern facing MPAs. The western Northern Channel Islands lie within the cool California Current while the eastern islands, of which Anacapa is one, are in the warmer Southern California Countercurrent (Hamilton et al. 2010). The sharp gradients between eastern and western islands in sea surface temperature, productivity, wind stress, and wave exposure put the Northern Channel Islands within three separate bioregions and within these regions the kelp forest fish community changes significantly (Harms and Winant 1998; Dever 2004; Blanchette et al. 2006, Hamilton et al. 2010). However, the bioregion and sea surface temperature are similar on both protected and unprotected sides of Anacapa Island as well as the eastern side of Santa Cruz Island (Hamilton et al. 2010). One transect for the greatest depth bin (>12-18 m) was conducted on the eastern side of Santa Cruz Island where fishing was permitted, and habitat conditions were comparable to those of the MPA location off Anacapa Island. This transect was conducted in order for a balanced depth design in MPA and non-MPA locations for this site, and to maintain surveys over similar habitat inside and outside MPAs. MPA and non-MPA areas were separated by at least 0.8 km.

Fish surveys within MPA and non-MPA locations were conducted during daylight hours (08:00-16:00) using belt-transects conducted on SCUBA (Brock 1954). Each site was surveyed during the same season and within a 7-day interval (one day for scouting similar reef habitat and six for surveys) to get a representative snapshot in time of the kelp forest fish community. For surveys, depth was standardized for both MPA and non-MPA locations at each site. Four transects were conducted within three depth bins of <6 m, 6-12 m, and >12-18 m, for a total of 12 replicate transects in each MPA and non-MPA per site. Before surveys, divers were trained on visually sizing fish to the nearest centimeter, and MPA and non-MPA locations were scouted for reefs with comparable substrate composition, relief, and kelp density. The outer edges of reefs were not surveyed to limit possible edge effects.

Downloaded from http://meridian.allenpress.com/scasbulletin/article-pdf/121/1/1/3078263/i2162-4534-121-1-1.pdf by guest on 23 December 2024

Fish surveys did not begin until comparable reefs were identified within the established depth bins for the MPA and non-MPA locations. Substrate composition was noted at the beginning and end of each transect, and number of *Macrocystis* holdfasts were counted within the first 10 m. Transects were haphazardly placed within the location area. Each underwater transect was composed of separate transects at three vertical regions of the water column (holdfast, mid-water, and canopy). Divers reeled out the 50 m transect behind them as they swam, identifying, counting, and visually estimating size to the nearest cm TL of transient and conspicuous fishes that occurred within the 50 x 2 x 1 m swath. The total volume surveyed per replicate, including the three depth strata was 300 m^3, over a benthic area of 100 m^2. Transects were separated from each other by at least 25 m to avoid surveying fish that may have moved between transects. Fish that swam up from behind the divers were not recorded during the survey to avoid recounting individuals. Holdfast and mid-water region transects were done simultaneously. To avoid recounting species that could possibly move between the two vertical regions during counts and keep a digital record of the transects, digital video transects (Ebeling et al. 1980a; b; Stephens et al. 1984; Larson and DeMartini 1984) were performed using a GoPro HD Hero2 camera during the mid-water transect, along with standard counts and size estimation. Video recordings of the mid-water videotransects were viewed and analyzed on the same day the transect was performed. Fishes that were video recorded moving between the vertical strata during the transect were removed from the second vertical strata to limit double counting fish schools on the transect. After conducting the holdfast and mid-water transects, the canopy region was surveyed using the same compass heading within 1-3 m of the surface.

In addition to estimating fish sizes to the nearest cm TL for each vertical stratum of the transect, "size surveys" within the transect area were obtained using parallel, length-calibrated lasers projected onto fishes and recorded with a mounted HD GoPro Hero2 video camera (Gingras et al. 1998; Colin et al. 2003; Heppell et al. 2012). Fish size surveys were conducted after each vertical region within the transect area to validate length estimations during the transect. Two sets of lasers were set at 2.6 and 10.2 cm apart and were accurate and visible up to 9 m underwater with good visibility. To reduce size estimation error fish were not measured at a distance greater than 2.5 m (Heppell et al. 2012). During fish size surveys, all fishes within the transect swath for each vertical region were targeted by the lasers and a video record was taken. Though an attempt was made to laser and video all fishes within the transect area, the species and sizes of the fish similar to those that occurred during the survey were targeted. In the lab, fish that occurred 90° to the video camera for each transect were sized (SL and TL cm) using the software program ImageJ (Fig. 2). As described in Pondella et al. (2019), lengths obtained from the size surveys were used for fishes counted during the corresponding transect and pass of similar estimated size. To determine biomass of each fish, lengths for each individual were converted to weights (gWwt) using length-weight relationships for each species (Table 2) and converted to biomass using the estimated transect area ($g/100m^2$). Analysis of the fish trophic structure included all conspicuous species ($n = 23$) observed during surveys. Several species occurred on transects that as adults are secondary carnivores, but as young-of-the-year are primary carnivores. Black and yellow rockfish (*Sebastes chrysomelas*), blue rockfish (*Sebastes mystinus*), chilipepper rockfish (*Sebastes goodei*), gopher rockfish (*Sebastes carnatus*), and California scorpionfish (*Scorpaena guttata*) were only observed as young-of-the-year, and thus considered primary carnivores. Also, young-of-the-year kelp bass <7 cm SL, juvenile sheephead, and young-of-the-year kelp rockfish were categorized as primary carnivores due to their feeding on zooplankton and other microinvertebrates

Downloaded from http://meridian.allenpress.com/scasbulletin/article-pdf/121/1/1/3078263/i2162-4534-121-1-1.pdf by guest on 23 December 2024

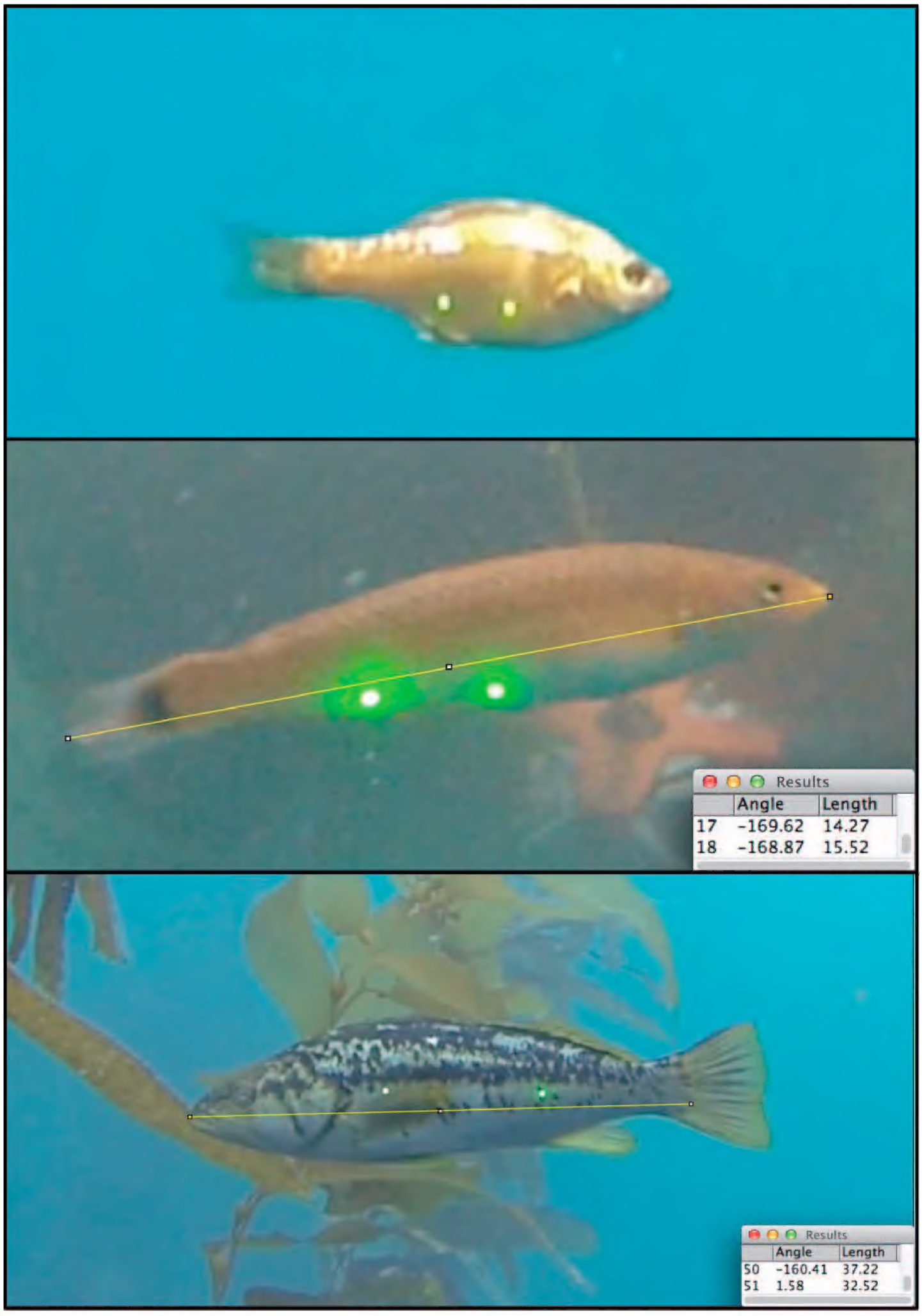


Fig. 2. Example images from video taken during size surveys using parallel lasers projecting spots onto fishes. Top: kelp perch with 2.5 cm spaced lasers. Middle: example of size estimation using the software program ImageJ. Image shows señorita measured with 2.5 cm spaced lasers and length (cm TL) being determined. Bottom: example of size estimation using the software program ImageJ. Image shows a measured kelp bass with 10.2 cm spaced lasers and length (cm SL) being determined.

Downloaded from http://meridian.allenpress.com/scasbulletin/article-pdf/121/1/1/3078263/i2162-4534-121-1-1.pdf by guest on 23 December 2024

Table 2. Equations used for each conspicuous kelp forest fish species to convert length (TL or SL) to gWwt (gram wet weight). Equations from Cailliet et al. (2000).

Species	Length/weight equations
kelp bass	$g\ Wwt = 0.000002716(mm\ TL)^{3.28}$
opaleye	$g\ Wwt = 0.00002(mm\ SL)^{3.08}$
halfmoon	$g\ Wwt = 0.000003(mm\ SL)^{3.454}$
señorita	$g\ Wwt = 0.00000128(mm\ SL)^{3.5}$
blacksmith	$g\ Wwt = 0.0000185(mm\ SL)^{3.09}$
California sheephead	$g\ Wwt = 0.00002952(mm\ TL)^{2.9066}$
garibaldi	$g\ Wwt = 0.000036(mm\ SL)^{3.10}$
kelp perch	$g\ Wwt = 0.00001184(mm\ SL)^{3.1686}$
black perch	$g\ Wwt = 0.00002(mm\ SL)^{3.149}$
rock wrasse	$g\ Wwt = 0.0000045(mm\ TL)^{3.16}$
shiner perch	$g\ Wwt = 0.000017(mm\ SL)^{3.125}$
olive rockfish	$g\ Wwt = 0.00000631(mm\ TL)^{3.136}$
kelp rockfish	$g\ Wwt = 0.0239(cm\ TL)^{2.862}$
blue rockfish	$g\ Wwt = 0.0158(cm\ TL)^{2.988}$
pile perch	$g\ Wwt = 0.0156(cm\ TL)^{2.998}$
rubberlip seaperch	$g\ Wwt = 0.00000457(mm\ SL)^{3.36}$
striped seaperch	$g\ Wwt = 0.0000000154(mm\ TL)^{3.01}$
California scorpionfish	$g\ Wwt = 0.0000398(mm\ SL)^{2.98}$
treefish	$g\ Wwt = 0.014(cm\ TL)^{3.081}$
gopher rockfish	$g\ Wwt = 0.0186(cm\ TL)^{2.957}$
chilipepper	$g\ Wwt = 0.0076(cm\ TL)^{3.12}$
barred sand bass	$g\ Wwt = 0.000006844(mm\ TL)^{3.1128}$

during this life stage. Transient pelagic fishes were recorded during surveys, but they were not included in analyses. It was assumed that these species use a variety of habitats and roam over large expanses of open ocean, and thus their assemblages would not differentially affect nor be affected by protection in MPAs. Hence, transient species were not included in analyses.

To analyze fluctuations in fish trophic structure abundance (numerical and biomass density) in relation to fishing pressure, each conspicuous fish species was grouped into a trophic level based on dietary habits and life stage according to Cross and Allen (1993). Trophic levels included in this study were herbivore/omnivore, primary carnivore, and secondary carnivore. The tertiary carnivore level included only giant sea bass, which was not observed during the surveys, and therefore, was not included in statistical analyses. Before analyses, a Shapiro-Wilk test (Shapiro and Wilk 1965) was used to test for homogeneity of variance among treatments. Biomass density ($g/100\ m^2$) was $\log_{10}(x+1)$ transformed to fit assumptions of normality. Numerical density ($\#/100\ m^2$) was square root transformed ($y' = \sqrt{y'}$) to meet assumptions and retain information regarding relative abundance (Clarke and Green 1988). We investigated fish trophic structure differences of the three trophic level biomass and numerical densities with a two-fixed factor sampling design (Site: 3 levels; Protection [MPA/non-MPA]: 2 levels) using multivariate analysis of variance (MANOVA). To evaluate the hypotheses that secondary carnivores decrease, primary carnivores increase, while herbivore/omnivores show no differences outside versus inside of MPAs, we performed three, two-factor univariate analysis of variances (ANOVAs) for each trophic level to the factors of site and protection with biomass and numerical

Downloaded from http://meridian.allenpress.com/scasbulletin/article-pdf/121/1/1/3078263/i2162-4534-121-1-1.pdf by guest on 23 December 2024

densities as response variables. MANOVA and ANOVAs were run in the statistical software program R (R Core Team 2013).

Furthermore, to address the hypothesis that lower abundance of large kelp bass (>25 cm) will correlate with higher abundance of specific prey species outside MPAs, and to investigate fishing effects at the species-level, we used PERMANOVA. Data for the analysis of the abundance of individual fish species inside and outside MPAs included many zeros, was positively skewed, and could not fit the assumption of normality required for parametric statistical testing. To analyze heterogeneous dispersions, which occur frequently in nature (Anderson and Millar 2004), the use of permutational methods allows ecologists to effectively analyze biological interactions in ecological communities. Univariate permutational analysis of variance with PERMANOVA+ for PRIMER-E ver. 6 (Anderson 2001; Anderson and Millar 2004) was used to test for differences in individual species' densities between the fixed factors of site and protection. PERMANOVA+ allows multivariate and univariate data to be tested by any resemblance matrix (e.g., Bray-Curtis dissimilarity), and all tests of hypotheses are done using permutations for robustness (Anderson et al. 2008). If there is only one variable in the analysis and Euclidean distances are used, then the PERMANOVA *F*-ratio is identical to the *F*-statistic (Fisher 1924) in traditional ANOVA (Anderson et al. 2008). However, the statistic used in PERMANOVA is the pseudo-*F*-statistic because it has an unknown distribution under a true null hypothesis (Anderson et al. 2008). Significant differences in PERMANOVA are determined as $P(\text{perm})<0.05$. Data was $\log_{10}$ (x+1) transformed for biomass densities and square root transformed for numerical densities. The resemblance matrix used in this study was calculated Euclidean dissimilarity distances for each species for 999 permutations. Eleven species were included in PERMANOVA biomass and numerical density analyses under the criteria of having a considerable abundance on reefs at all sites, being potential target species in the recreational fishery, and/or prey species to piscivorous fishes. Of the eleven species, kelp bass were categorized into three size/age classes; YOY = <7 cm, Small = 7-25 cm, and Large = >25 cm SL. Sheephead were categorized by three gender/life stages, namely Juvenile, Female, and Male.

Results

Multivariate analysis for numerical densities (#/100 m^2) of the three trophic levels showed significant differences in relation to the two factors Site ($F = 6.47$, $p < 0.001$) and Protection ($F = 15.87$, $p < 0.001$). Differences among sites were largely attributed to lower numerical densities at the mainland site (La Jolla) in comparison to the two island sites (Catalina and Anacapa). Numerical densities for La Jolla were 3.7× less than Catalina and 1.7× less than Anacapa. Further univariate analyses of each trophic level revealed that herbivore/omnivores (Fig. 3) had lower numerical densities outside of MPAs ($F = 8.69$, $p = 0.004$). Similarly, secondary carnivores (Fig. 3) had lower densities outside of MPAs ($F = 23.67$, $p < 0.001$), as well as showed differences in abundance among sites ($F = 8.33$, $p < 0.001$). Site differences for secondary carnivores were likely due to higher total numerical densities observed at Catalina compared to La Jolla (2×) and Anacapa (1.6×). In an inverse trend to the secondary carnivores and herbivore/omnivores, the primary carnivores (Fig. 3) showed a non-significant trend in higher numerical densities outside of MPAs ($F = 3.22$, $p = 0.07$). A significant difference among sites was observed ($F = 23.57$, $p < 0.001$). Differences among sites were attributed to total numerical densities at Catalina being higher than both La Jolla (3.5×) and Anacapa (2×). Mean numerical densities

Downloaded from http://meridian.allenpress.com/scasbulletin/article-pdf/121/1/1/3078263/i2162-4534-121-1-1.pdf by guest on 23 December 2024

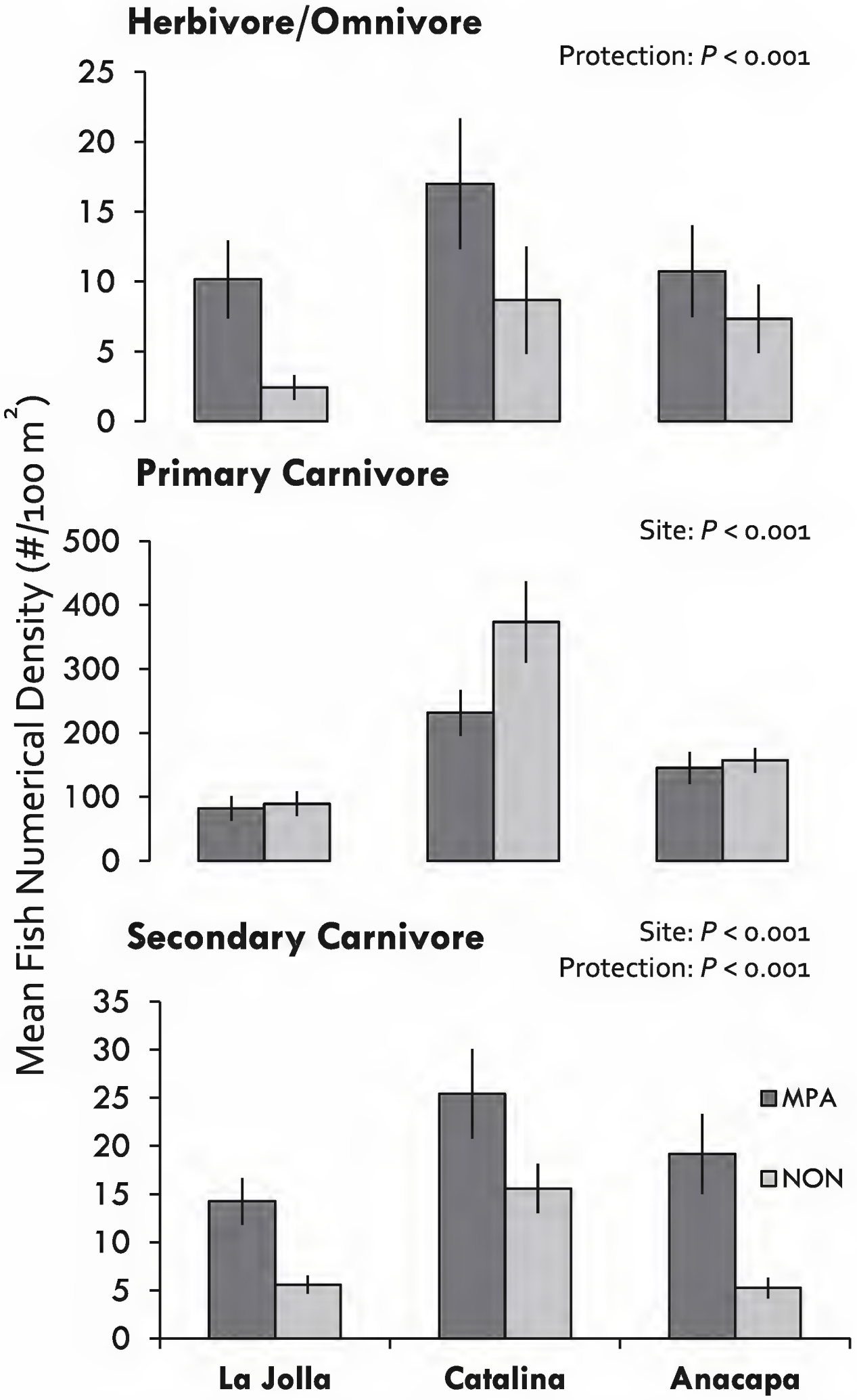


Fig. 3. Differences in mean numerical densities of fishes in the three trophic levels per site.

Downloaded from http://meridian.allenpress.com/scasbulletin/article-pdf/121/1/1/3078263/i2162-4534-121-1-1.pdf by guest on 23 December 2024

(Fig. 3) were higher inside MPAs for herbivore/omnivore (12.64 ± 2.12 #/100 m^2) and secondary carnivore (19.61 ± 2.3 #/100 m^2) trophic levels compared to corresponding non-MPA locations (herbivore/omnivore: 6.14 ± 1.57 #/100 m^2; secondary carnivore: 8.8 ± 1.25 #/100 m^2). Primary carnivores showed a trending inverse relationship of overall lower mean numerical densities inside MPAs (152.94 ± 18.67 #/100 m^2) compared to non-MPAs (206.64 ± 30.4 #/100 m^2).

Biomass densities (g/100 m^2) of the fish community showed stronger contrasts among trophic levels due to protection than numerical densities. Multivariate analysis of the three trophic levels (Fig. 4) differed with the main effects of Site ($F = 9.19$, $p < 0.001$) and Protection ($F = 13.02$, $p < 0.001$). Site differences in trophic structure were attributed to considerably lower biomass densities between La Jolla and Catalina/Anacapa. Biomass densities for La Jolla were 2.6x less than Catalina and 3.1x less than Anacapa. Univariate analyses for the biomass densities of each trophic level (Fig. 4) showed results similar to numerical densities, where herbivore/omnivores ($F = 10.36$, $p = 0.002$) and secondary carnivores ($F = 32.97$, $p < 0.001$) significantly decreased outside of MPAs. The secondary carnivore level also showed differences between sites ($F = 10.38$, $p < 0.001$), as overall biomass densities among sites were different, but displayed similar patterns inside and outside of MPAs. The primary carnivores (Fig. 4) exhibited an opposite pattern with biomass being significantly higher outside MPAs ($F = 4.23$, $p = 0.04$). Primary carnivore biomass also differed between sites ($F = 38.63$, $p < 0.001$), and was likely attributed to higher overall biomass between the island sites (Catalina and Anacapa) and the mainland site (La Jolla). Mean biomass inside MPAs of herbivore/omnivores (7.90 ± 1.44 kg/100 m^2) and secondary carnivores (10.26 ± 1.65 kg/100 m^2) were higher compared to non-MPA locations (herbivore/omnivore: 2.68 ± 0.71 kg/100 m^2; secondary carnivore: 1.95 ± 0.32 kg/100 m^2). Primary carnivores had a lower mean biomass inside MPAs (4.49 ± 0.55 kg/100 m^2) in contrast to non-MPAs (6.78 ± 0.93 kg/100 m^2).

Two of the three target secondary carnivores showed significantly lower abundances outside MPAs as well as biogeographic differences per site. Sheephead (Fig. 5) were grouped by males, females, and juveniles. Male sheephead numerical densities were significantly lower outside of MPAs (pseudo-$F = 24.03$, $P_{(perm)} < 0.001$) with a significant interaction between site and protection (pseudo-$F = 3.95$, $P_{(perm)} = 0.03$), attributed to a non-significant decrease outside of MPAs in La Jolla. Biomass of male sheephead followed a similar trend (pseudo-$F = 29.26$, $P_{(perm)} < 0.001$) with an interaction (pseudo-$F = 3.99$, $P_{(perm)} = 0.023$). Overall, large male sheephead were almost exclusively found in MPAs. Female sheephead biomass and numerical densities (Fig. 5) did not significantly differ across sites or due to protection. Juvenile sheephead showed a difference among sites for both numerical (pseudo-$F = 22.81$, $P_{(perm)} < 0.001$) and biomass densities (pseudo-$F = 19.03$, $P_{(perm)} < 0.001$).

The most abundant piscivore, kelp bass (Fig. 6) numerical and biomass densities showed a large decrease outside of MPAs for individuals >25 cm (numerical densities: pseudo-$F = 30.16$, $P_{(perm)} < 0.001$; biomass: pseudo-$F = 28.84$, $P_{(perm)} < 0.001$). Kelp bass 7-25 cm showed differences in relation to sites (numerical densities: pseudo-$F = 19.93$, $P_{(perm)} < 0.001$; biomass: pseudo-$F = 8.63$, $P_{(perm)} = 0.002$) and had lower densities outside of MPAs (numerical densities: pseudo-$F = 8.37$, $P_{(perm)} = 0.009$; biomass: pseudo-$F = 6.19$, $P_{(perm)} = 0.02$). Kelp bass 7-25 cm also had a significant interaction effect for biomass densities (pseudo-$F = 3.28$, $P_{(perm)} = 0.046$), as there was no significant difference in biomass between MPAs and non-MPAs for Catalina. Kelp bass <7 cm showed strong differences among sites (numerical densities: pseudo-$F = 68.72$, $P_{(perm)} < 0.001$; biomass:

Downloaded from http://meridian.allenpress.com/scasbulletin/article-pdf/121/1/1/3078263/i2162-4534-121-1-1.pdf by guest on 23 December 2024

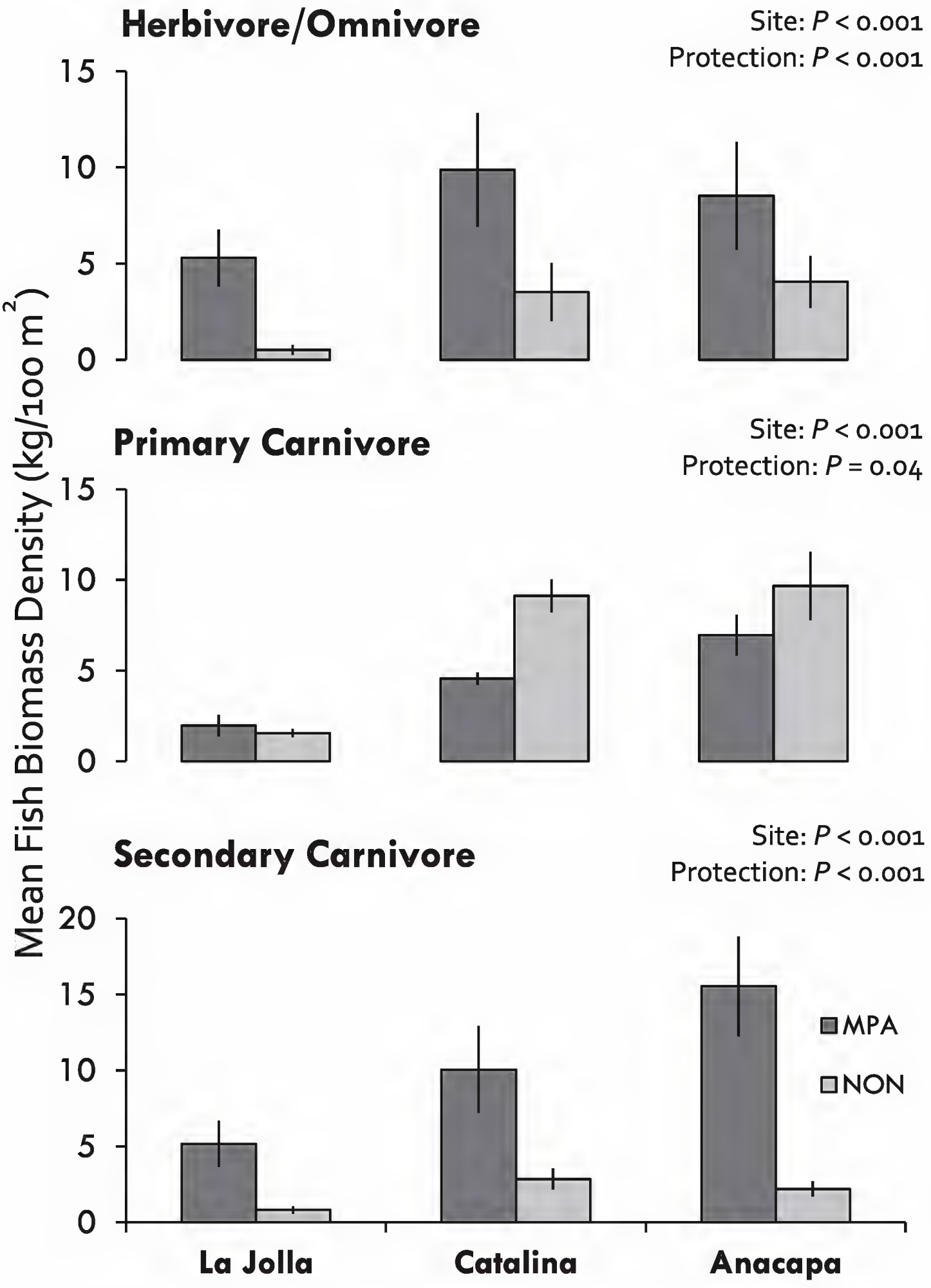


Fig. 4. Differences in mean biomass densities of fishes in the three trophic levels per site.

Downloaded from http://meridian.allenpress.com/scasbulletin/article-pdf/121/1/3078263/i2162-4534-121-1-1.pdf by guest on 23 December 2024

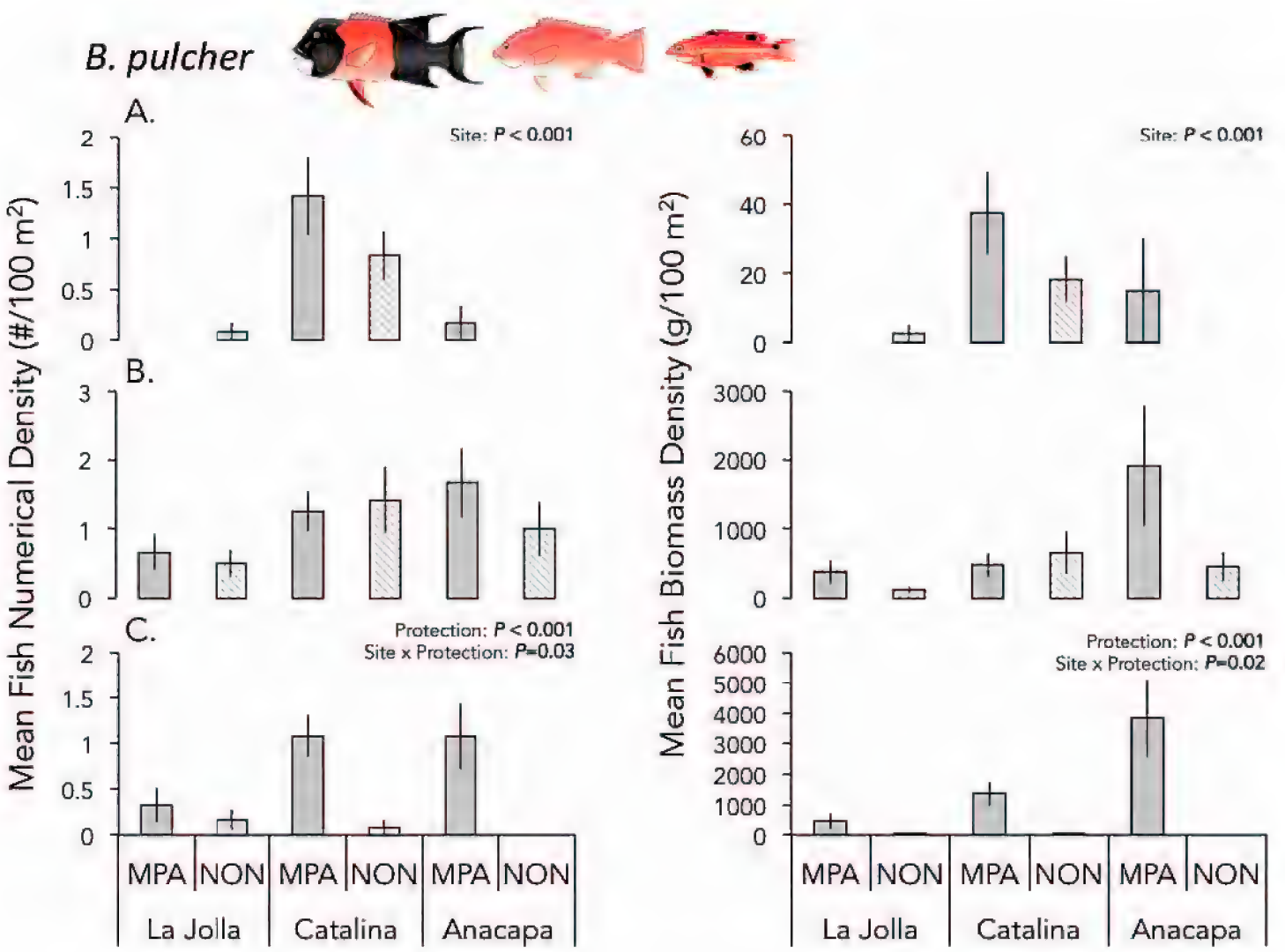


Fig. 5. California sheephead (*Bodianus pulcher*) mean numerical and biomass density among sites and between protection status (MPA and Non-MPA). A = Juvenile, B = Female, C = Male.

pseudo-$F = 50.63$, $P_{(perm)} < 0.001$) with a significant interaction (numerical densities: pseudo-$F = 6.85$, $P_{(perm)}) = 0.004$; biomass: pseudo-$F = 6.93$, $P_{(perm)} = 0.003$), as overall densities were considerably greater at Catalina and in the non-MPA location for that site. However, no discernible pattern inside and outside MPAs for kelp bass <7 cm was consistently found among the three sites.

Of the primary carnivores included in species level analysis, two of the species (black perch and garibaldi) were included for being abundant during surveys, occurring at all sites, and for potential population regulation by kelp bass due to predation on recruits. Black perch (Fig. 7) significantly differed among sites for both numerical (pseudo-$F = 5.14$, $P_{(perm)} = 0.02$) and biomass densities (pseudo-$F = 4.6$, $P_{(perm)} = 0.005$), and a significant interaction (numerical densities: pseudo-$F = 4.45$, $P_{(perm)} = 0.02$; biomass: pseudo-$F = 4.13$, $P_{(perm)} = 0.01$), due to large disordered fluctuations inside and outside of MPAs. Likewise, garibaldi (Fig. 8) only differed among sites in numerical (Table 9: pseudo-$F = 9.6$, $P_{(perm)} < 0.001$) and biomass densities (pseudo-$F = 6.1$, $P_{(perm)} < 0.001$), as a total higher abundance was observed at Catalina compared to La Jolla and Anacapa.

The four fishes included in the species level analysis as prey species for large kelp bass (Fig. 8: kelp perch, blacksmith, señorita; Fig. 10: rock wrasse) showed varying relationships for the factors site and protection. Both blacksmith (Fig. 8) and rock wrasse (Fig. 9) showed no significant pattern related to protection. The abundance of blacksmith differed to site in numerical (pseudo-$F = 15.94$, $P_{(perm)} < 0.001$) and biomass densities (pseudo-$F = 12.5$, $P_{(perm)} < 0.001$), with high numbers of recruits at Catalina and

Downloaded from http://meridian.allenpress.com/scasbulletin/article-pdf/121/1/1/3078263/i2162-4534-121-1-1.pdf by guest on 23 December 2024

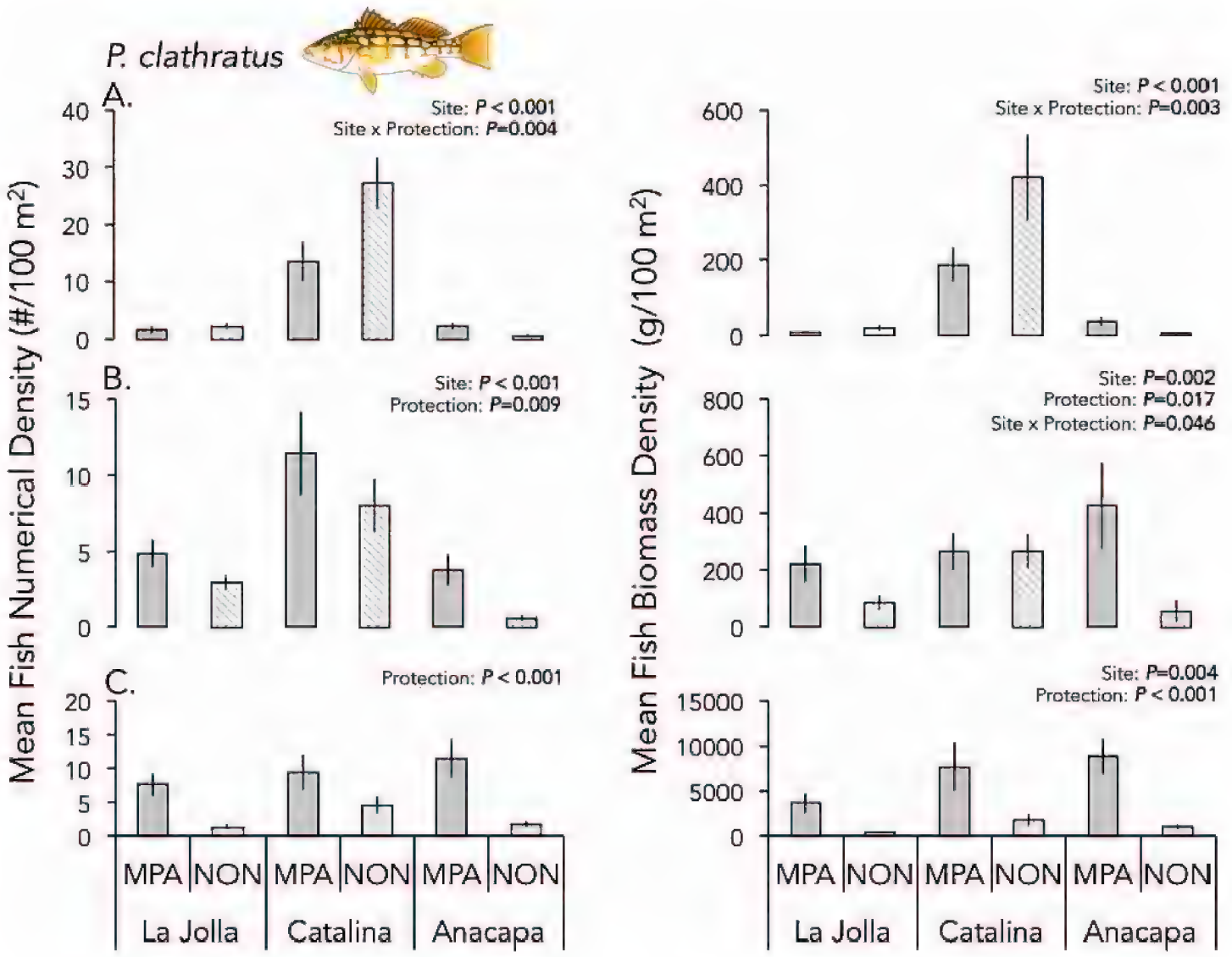


Fig. 6. Kelp bass (*Paralabrax clathratus*) mean numerical and biomass density among sites and between protection status (MPA and Non-MPA). A = < 7 cm, B = 7 - 25 cm, C = > 25 cm.

larger individuals at the Anacapa non-MPA location. Rock wrasse biomass was significantly different among sites (pseudo-F = 7.35, $P_{(perm)}$ = 0.001). There also was a significant interaction for rock wrasse (numerical densities: pseudo-F = 8.12, $P_{(perm)}$ = 0.002; biomass: pseudo-F = 10.08, $P_{(perm)}$ = 0.001), attributed to inconsistent differences inside versus outside of MPAs per site. Señorita (Fig. 8) numerical densities showed no significant effect to protection or site. On the other hand, señorita biomass was significantly different in respect to site (pseudo-F = 6.24, $P_{(perm)}$ = 0.003), as much higher biomass was observed at Anacapa compared to La Jolla and Catalina. Likewise, señorita showed a trend of larger individuals and higher biomass outside of MPAs. However, this increase was not statistically significant (pseudo-F = 3.75, $P_{(perm)}$ = 0.052). Kelp perch (Fig. 8) numerical densities were significantly higher outside of the MPAs (pseudo-F = 6.94, $P_{(perm)}$ = 0.012). However, the trend in higher kelp perch biomass outside MPAs among sites was not significant (pseudo-F = 2.92, $P_{(perm)}$ = 0.08).

Two of the three species within the herbivore/omnivore level were included in species level analysis for having high abundances on surveys and occurring at all three sites. Halfmoon (Fig. 9) showed no significant differences in relation to protection or sites for both numerical and biomass densities. On the other hand, opaleye (Fig. 9) followed a similar pattern to target secondary carnivore species, with lower numerical (pseudo-F = 8.99, $P_{(perm)}$ = 0.007) and biomass densities (pseudo-F = 11.91, $P_{(perm)}$ = 0.002) outside MPAs.

Downloaded from http://meridian.allenpress.com/scasbulletin/article-pdf/121/1/1/3078263/i2162-4534-121-1-1.pdf by guest on 23 December 2024

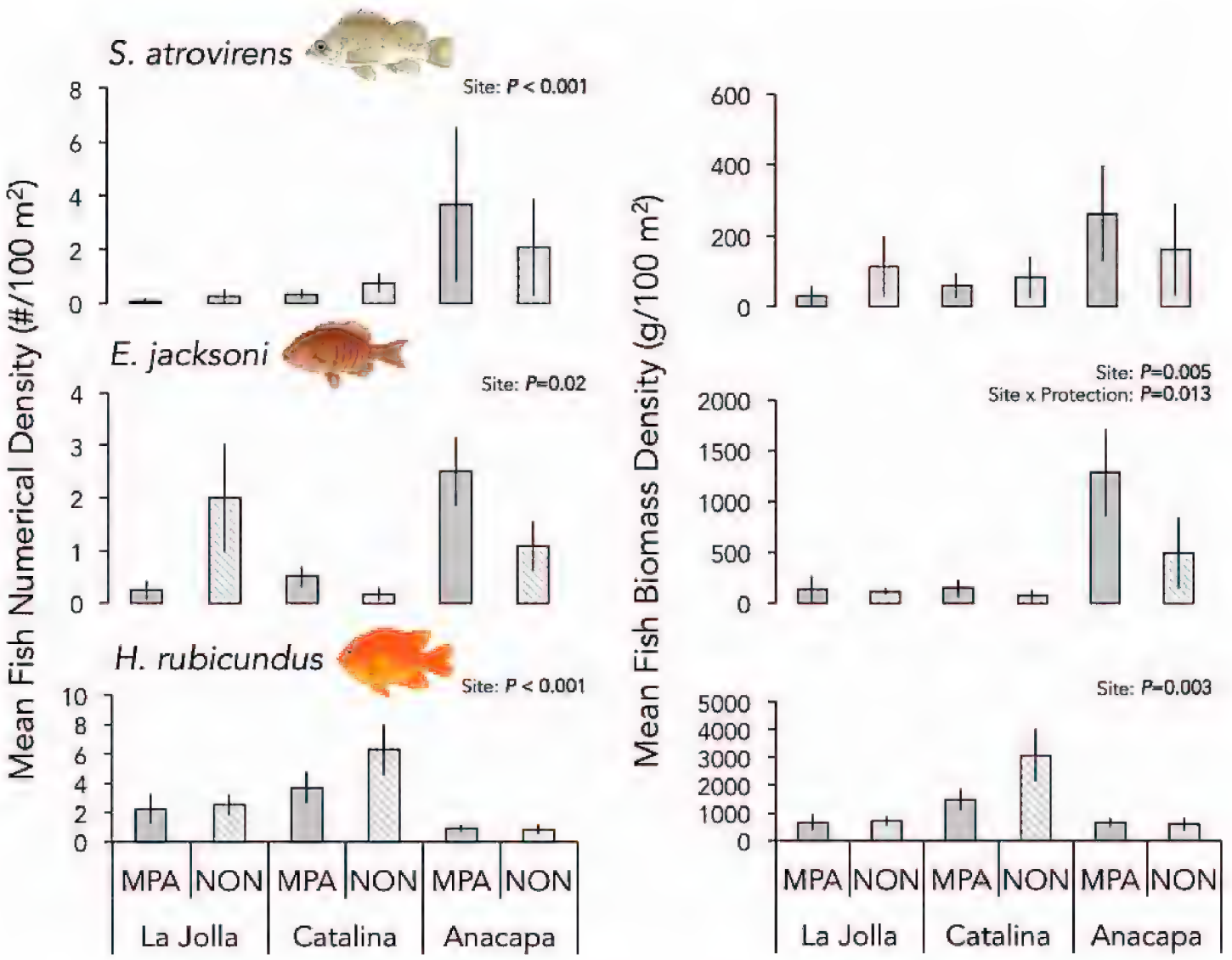


Fig. 7. Mean numerical and biomass density of kelp rockfish (*Sebastes atrovirens*), black perch (*Embiotoca jacksoni*), and garibaldi (*Hypsypops rubicundus*) among sites and between protection status (MPA and Non-MPA).

Discussion and Conclusions

The results of this study provide several insights into the direct and indirect impacts of fishing on the kelp forest fish community throughout a wide geographic range within the Southern California Bight. Overall, numerical and biomass densities within trophic levels differed among sites and protection (inside and outside MPAs). Secondary carnivores had higher biomass (5.3×) and densities (2.2×) inside MPA locations at all three sites, providing support for our first hypothesis that the secondary carnivore trophic level will be lower outside of MPAs from lack of protection. This result was expected as the secondary carnivores included several important target species in the southern California recreational fishery. The greater decrease of biomass relative to numerical densities for secondary carnivores outside MPAs was attributed to smaller individuals outside of the MPAs coupled with lower numerical densities.

In the absence of large piscivores, smaller prey fishes can grow to larger body sizes (DeMartini et al. 2008) and can potentially allow them to escape predation (Mumby et al. 2006). In an inverse pattern to predatory secondary carnivores, the primary carnivore trophic level was significantly higher in biomass densities (1.5×) outside of MPAs, supporting the second hypothesis that primary carnivores, which consist of many smaller prey fishes, would increase outside of MPAs. However, this hypothesis was only partially supported, as the slight trend of increasing densities outside MPAs (1.3×) was not significant

Downloaded from http://meridian.allenpress.com/scasbulletin/article-pdf/121/1/1/3078263/i2162-4534-121-1-1.pdf by guest on 23 December 2024

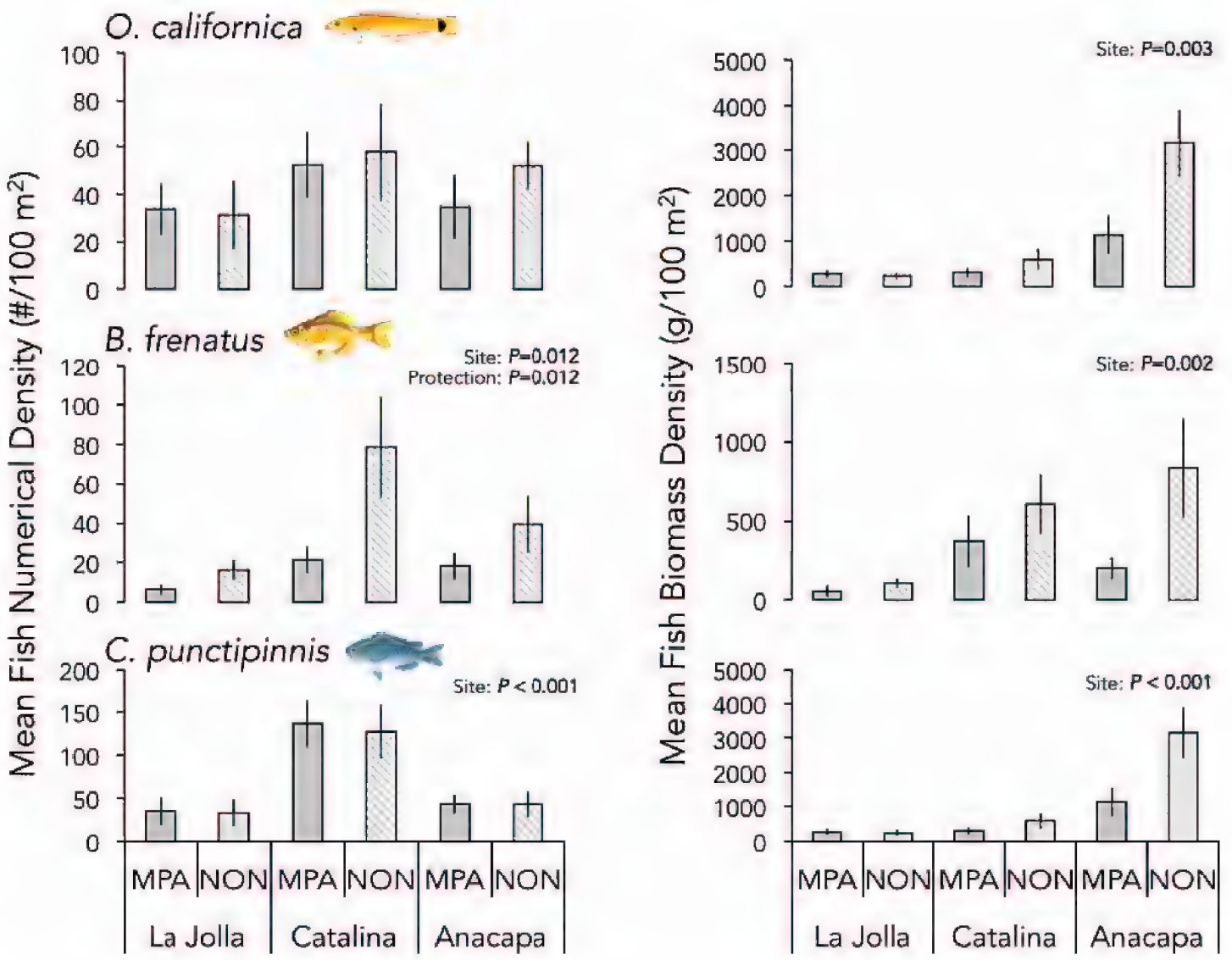


Fig. 8. Mean numerical and biomass density of señorita (*Oxyjulis californica*), kelp perch (*Brachyistius frenatus*) and blacksmith (*Chromis punctipinnis*) among sites and between protection status (MPA and Non-MPA).

for the trophic level. This suggests that the primary carnivores as a whole were larger in body size outside MPAs, and though increases were observed in numerical densities, these were not significant. Herbivore/omnivores had unexpectedly lower biomass (3.0×) and numerical densities (2.0×) outside MPAs in a similar fashion to secondary carnivores. This decrease of the herbivore/omnivore level further confounded a full acceptance of the second hypothesis, as no change was expected due to the larger body size of these species, which should protect them from predation by reef associated piscivorous fishes, and for not being targeted in the southern California recreational fishery.

There were considerable differences in both numerical and biomass densities among the three sites. This was largely attributed to biogeographic differences, where lower overall numerical and biomass densities occurred at the mainland site (La Jolla) compared to island sites (Catalina and Anacapa Island). Likewise, at La Jolla, the abundance of primary carnivores was similar inside and outside of the MPA. While, Catalina contained the largest number of recruits both in MPA and non-MPA locations showing much higher densities at this site. Furthermore, Anacapa contained higher biomass densities among the secondary carnivores due to much larger sheephead and kelp bass. Thus, the biomass density of secondary carnivores was highest at Anacapa compared to Catalina and La Jolla although numerical densities were not as high. Despite these site differences, a strikingly similar pattern in the overall trophic structure biomass was observed in MPA and

Downloaded from http://meridian.allenpress.com/scasbulletin/article-pdf/121/1/1/3078263/i2162-4534-121-1-1.pdf by guest on 23 December 2024

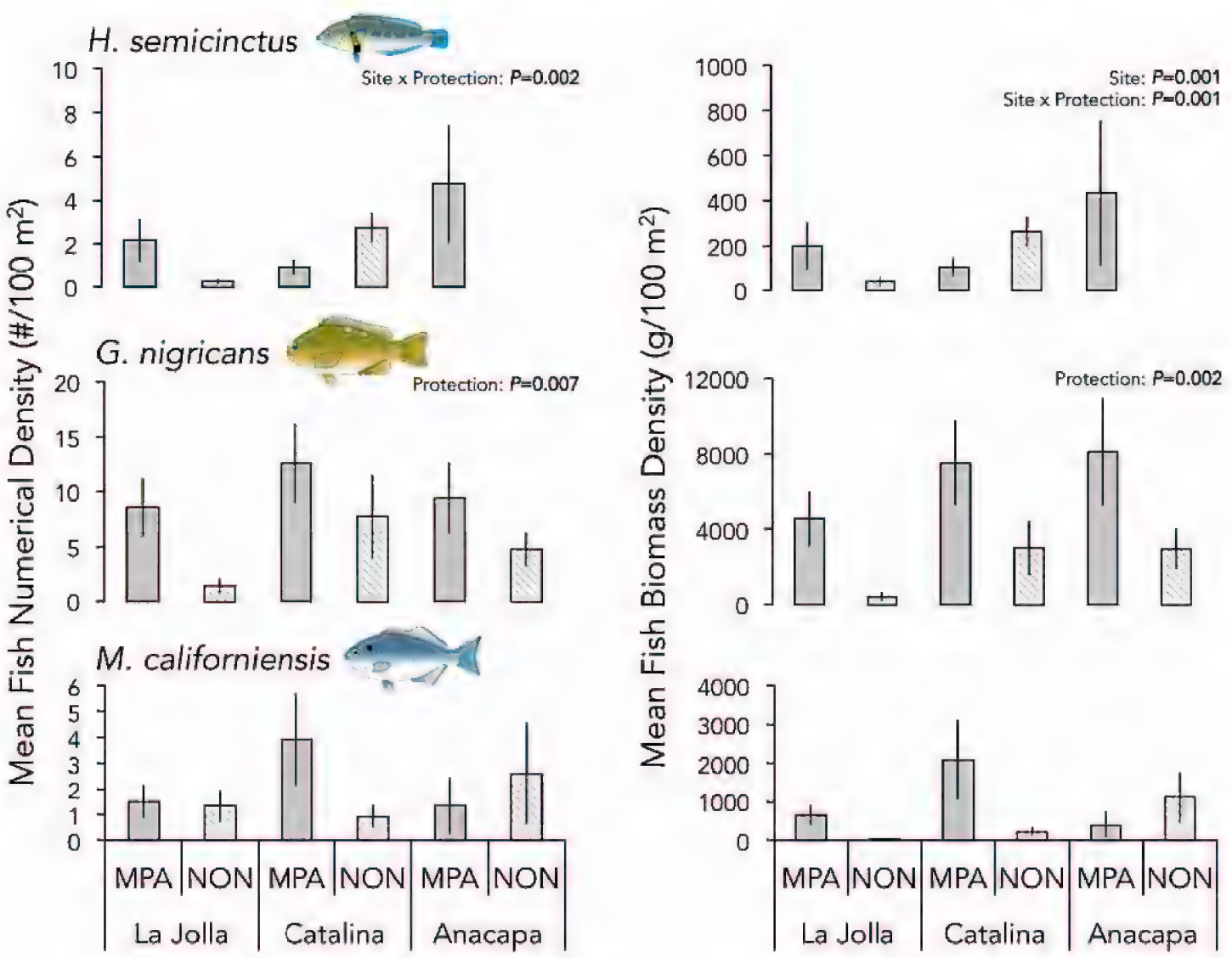


Fig. 9. Mean numerical and biomass density of rock wrasse (*Halichoeres semicinctus*), opaleye (*Girella nigricans*) and halfmoon (*Medialuna californiensis*) among sites and between protection status (MPA and Non-MPA).

non-MPA locations. At each site, secondary carnivores and herbivore/omnivores dominated the trophic fish biomass within the MPAs. On the other hand, the primary carnivores dominated the fish biomass outside of protection in the non-MPA locations (Fig. 4). This was attributed to several combined increases of planktivorous and mesograzer species or overall biomass stability (La Jolla) within the primary carnivore trophic level and decreases of target secondary carnivores and abundant herbivore/omnivores. This pattern suggests a fishing induced shift in the trophic structure of kelp forest fishes outside of protected areas. However, these findings are in contrast to those found in the marine reserve meta-analysis by Halpern (2003) where all functional groups (invertebrates, herbivorous fishes, planktivores/invertebrate eating fishes, and carnivorous fishes) increase inside MPAs in almost all cases. However, an explanation for this result could be that the detection of top down control or trophic cascades within a community could be masked when analyzing a large number of species (Polis and Strong 1996; Halpern 2003). In addition, these results are different than those of Hamilton et al. (2010) who found that after the first five years of protection in the northern Channel Islands marine reserve network, piscivore and other carnivore functional groups increased within the reserves, but no discernible difference was detected for planktivores or herbivores relative to protection. However, Hamilton et al. (2010) found differences in community structure over relatively small spatial scales due to differences in sea surface temperature and other environmental changes among the

Downloaded from http://meridian.allenpress.com/scasbulletin/article-pdf/121/1/1/3078263/i2162-4534-121-1-1.pdf by guest on 23 December 2024

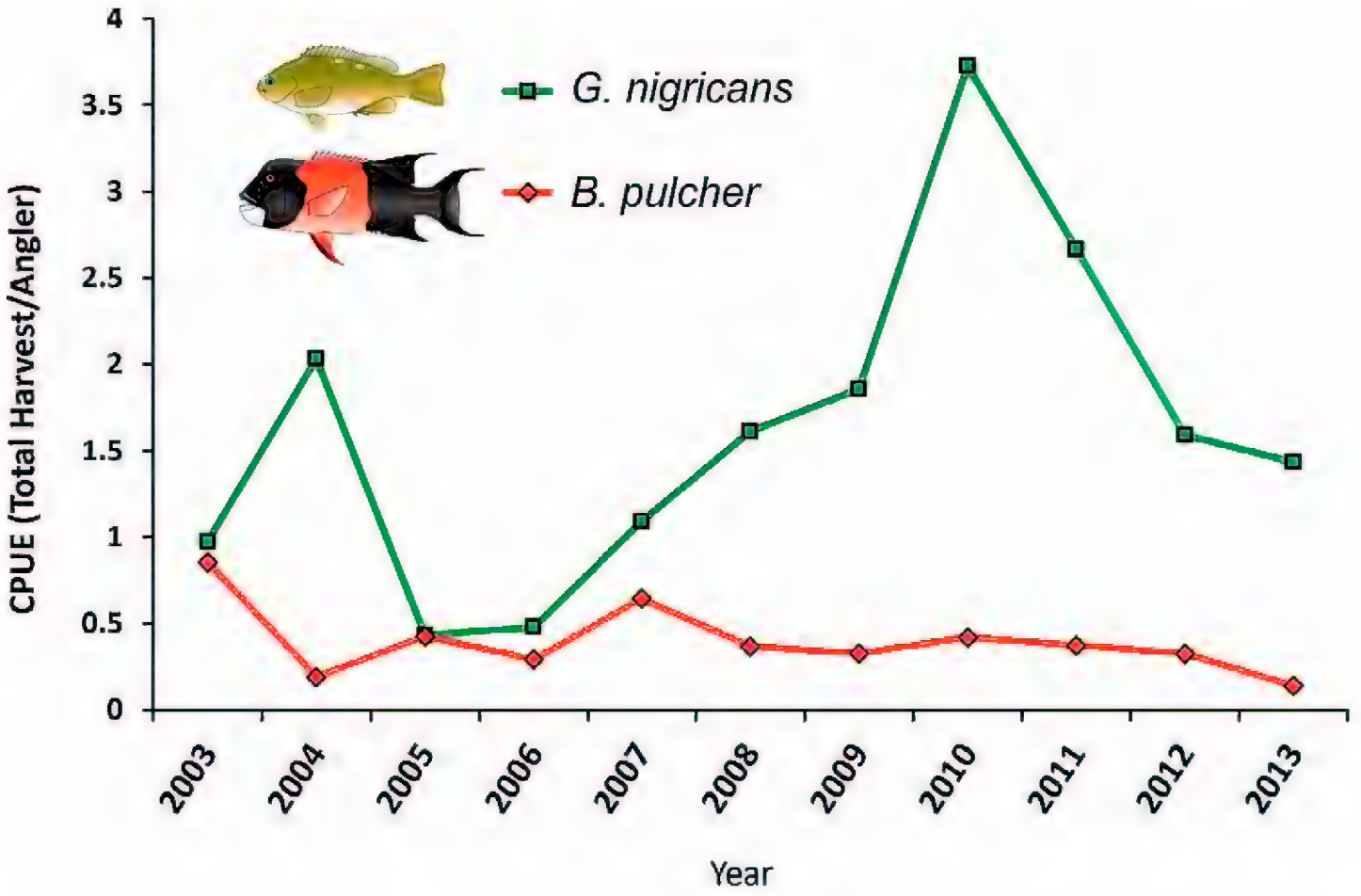


Fig. 10. Total fish harvested per number of anglers (CPUE) from the years 2003-2013 for opaleye (*Girella nigricans*) = green, and sheephead (*Bodianus pulcher*) = red. Data from RecFIN, the Recreational Fisheries Information Network(https://www.recfin.org).

northern Channel Islands. It is also possible that Hamilton et al. (2010) were unable to detect lower trophic level effects because of the shorter time period in which the reserve network had been established. Despite these conclusions, top down influences have been observed in relation to fishing pressure on the level of trophic/functional groups (Daskalov et al. 2007) and in extensive analysis of species within communities (Watson et al. 2007). In the Black Sea, Daskalov et al. (2007) showed decreases in the overall trophic group of piscivores led to a dominant abundance of planktivorous fishes. While in the temperate-tropical transition zone off the Abrolhos Islands, Watson et al. (2007), documented that lower abundance of five prominent smaller-bodied reef fishes was likely related to increases of target piscivores inside MPAs. The findings of this study are indicative of trophic structure changes in relation to fishing pressure within the southern Californian kelp forest fish community with decreases in larger secondary carnivore predators and herbivore/omnivores and increases in smaller bodied primary carnivores.

Changes in individual populations fluctuated to varying degrees in MPA and non-MPA locations. Of target secondary carnivores included in the species level analysis, two of the three species showed decreases in fished locations. The effect of fishing on the target invertivore, sheephead, differed among life stages (Fig. 5). Male sheephead densities (10×) and biomass (96.1×) were much lower outside MPAs. This large difference was because most individuals were much larger and almost exclusively observed in MPAs (e.g., no male sheephead were observed during Anacapa non-MPA surveys). However, neither females nor juveniles showed discernible differences or patterns relative to protection. Of the two abundant piscivores (kelp bass and kelp rockfish), only kelp bass were influenced by fishing as no apparent pattern was observed for kelp rockfish. Large legal-size kelp bass

Downloaded from http://meridian.allenpress.com/scasbulletin/article-pdf/121/1/1/3078263/i2162-4534-121-1-1.pdf by guest on 23 December 2024

(>25 cm SL) greatly decreased in numerical (3.7×) and biomass (6.5×) densities outside MPAs at each site. Smaller kelp bass 7-25 cm SL followed a milder decrease outside of MPAs. However, this trend was not apparent at Catalina. Kelp bass young-of-the-year <7 cm SL showed site-specific differences, but not relative to protection. The dramatic response of large target fishes to protection from fishing is in concordance with the numerical and biomass density findings of previous studies in southern California kelp forests (Halpern 2003; Froeschke et al. 2006; Tetreault and Ambrose 2007; Eisaguirre et al. 2021).

An unexpected result from the trophic structure analysis was the decrease in the herbivore/omnivore trophic level outside MPAs. Two abundant species within this trophic level are the opaleye and halfmoon (Fig. 9). Halfmoon presence was considerably less than opaleye, and besides being largely abundant in the MPA location at Catalina and smaller individuals in La Jolla, halfmoon did not appear to benefit from the protection afforded by the MPAs. On the other hand, the more abundant opaleye, had consistently lower numerical (2.1×) and biomass densities (3.2×) outside MPAs. Due to their large body size reaching up to 65 cm TL and 6 kg, predation by kelp bass should not have a large effect on adult opaleye reef populations. However, it is possible that decreases in target species (sheephead and kelp bass) that could be preferred food for predators with larger home-ranges than set MPA boundaries (i.e. pinnipeds, soupfin sharks, angel sharks, Brandt's cormorants, and/or giant sea bass) or cryptic reef predators (California moray eel), could switch to a more accessible prey (Murdoch et al. 1975). Recreational fishing for opaleye was also expected to have little effect on population size as they are categorized as an "incidental-catch" species and therefore not targeted by anglers. However, from the years 2003-2013 mean total recreational catch of opaleye off southern California (56,060 ± 6,866) was as high if not higher than several target species such as olive rockfish (21,298 ± 5,363), kelp rockfish (17,588 ± 4,103), as well as the highly sought after sheephead (49,504 ± 4,215). Comparing sheephead and opaleye CPUE (Fig. 12), a steady decrease in catch was seen in sheephead from 2003-2013. However, the trend in opaleye CPUE is harder to discern. After a peak in 2004 and subsequent decrease in 2005, there was a strong increase in CPUE from 2006-2010, with sharp decreases until 2013. Altogether, the mean number of harvested opaleye per angler is 4.1× that of sheephead, suggesting that though they may not be a target species they are taken in considerable number by anglers in southern California. However, there are still other explanations for opaleye decreases in areas outside MPAs. The increase of large bodied reef associated herbivores inside MPAs has also been documented in other ecosystems (Mumby et al. 2006; Watson et al. 2007). It is possible that large-bodied herbivores can escape predation by reef piscivores (Mumby et al. 2006), and possibly out compete less abundant smaller bodied individuals for habitat and food within MPAs (Watson et al. 2007). In addition, a possible explanation to this pattern could be of fine-scale habitat characteristics that are difficult to detect (Watson et al. 2007). MPA and non-MPA locations were surveyed in similar substrate composition and kelp density at each site, and opaleye are commonly found in deforested reefs (Graham 2004), suggesting kelp presence to not be a definitive factor for population abundance. However, other possibilities could be that of spatial secondary habitat characteristics that were not detected during this study. Opaleye appear to show a preference for large reefs in close proximity to adjoining reefs (E. Parnell unpub. data). As many MPAs are selected for areas rich in available habitat for many reef fishes, the overall size and proximity of individual reefs and the distance to each other could also influence opaleye population abundances.

Downloaded from http://meridian.allenpress.com/scasbulletin/article-pdf/121/1/1/3078263/i2162-4534-121-1-1.pdf by guest on 23 December 2024

Direct removals of predators can indirectly release top-down pressure on prey populations. As evidenced from previous studies in other marine ecosystems (Mueter and Norcross 2000; Dulvy et al. 2004; Blanchard et al. 2005; Daan et al. 2005; Frank et al. 2005; Watson et al. 2007; DeMartini et al. 2008; Davis et al. 2019), our study found an indirect effect of fishing by observed increases of a non-target prey species, and the primary carnivore trophic level, in areas subject to fishing pressure. Kelp perch numerical densities significantly increased (2.9×) in non-MPA locations. This result is likely due to strong decreases in fished areas of large kelp bass in fished areas, the primary piscivore of this system. This suggests a possible release in top-down control by kelp bass on the kelp perch population and provides support for the third hypothesis that decreases in large >25 cm piscivorous kelp bass correlates with increases in prey reef fishes outside MPAs. Fluctuations in abundance of kelp perch could further influence ecosystem dynamics on the primary producer level (Davenport and Anderson 2007). However, the biomass densities of kelp perch showed a non-significant increase outside MPAs. The higher numerical densities compared to biomass outside MPAs was attributed to more juveniles and smaller individuals being present in non-MPA locations compared to larger adults in MPAs, possibly large enough to evade predation by smaller kelp bass. Likewise, another prey reef fish, señorita, showed a non-significant trend of higher biomass densities (2.3×) and overall larger individuals outside of MPAs. This is a trend that if biologically significant could likewise affect kelp forest structure. Señorita, similar to kelp perch, are important predators of mesograzers that feed on *Macrocystis* blades and fluctuations in the abundance of these fish could either alleviate pressure on *Macrocystis* from mesograzers (Bernstein and Jung 1979; Davenport and Anderson 2007), or decimate kelp forests while feeding on encrusted blades (Bernstein and Jung 1979). Similar to these results, Tetreault and Ambrose (2007) found a trend toward higher señorita biomass outside of MPAs. However, they provided little information on kelp perch densities. The fourth prey species analyzed, rock wrasse, showed no discernible pattern in relation to fishing pressure. Likewise, no pattern was detected among sites for black perch and garibaldi in and out of MPAs.

Empirical studies have shown that large piscivores affect the abundance of prey reef fishes (Doherty and Sale 1985; Caley 1993; Carr and Hixon 1995; Hixon and Carr 1997). Additionally, there is experimental support for kelp bass influencing abundance and distributions of local populations and post settlement juveniles of kelp forest fishes (Carr 1991; Steele 1997b; Steele 1998; Steele 1999; Anderson 2001) therefore potentially effecting community dynamics. In particular, Anderson (2001) found that aggregative predation responses of kelp bass negatively affected numerical densities of kelp perch. However, there has yet been a study detecting an increase of prey reef fish assemblages due to kelp bass decreases in areas subject to fishing (Tetreault and Ambrose 2007; Hamilton et al. 2010). A possible answer could lie in the life history of the kelp perch. Kelp perch were found throughout the water column in kelp forests; however, juveniles tend to seek shelter in the kelp canopy. Tetreault and Ambrose (2007) surveyed in and out of five MPAs throughout southern California (several of which have now changed or consolidated), but underwater belt transects for estimating fish abundance and size were located on the benthos (holdfast region), and could likely fail to survey key species residing in the kelp canopies and midwater column. Also, a survey method was implemented in this study that provided more precise size estimations by reducing diver size estimation error. We used parallel length calibrated lasers mounted on a video camera for high resolution size surveys after transect counts. Another explanation for these findings besides variability in survey methods could be fluctuations of overall community dynamics in the 15 years

Downloaded from http://meridian.allenpress.com/scasbulletin/article-pdf/121/1/1/3078263/i2162-4534-121-1-1.pdf by guest on 23 December 2024

since Tetreault and Ambrose (2007). Indirect effects of fishing could take decades to manifest (Daan et al. 2005; Babcock et al. 2010; Estes et al. 2011). This lag could explain a more recent change in the fish community makeup as differences between protected and nearby unprotected areas greaten over time. However, arguably the preeminent difference may be the return of the apex tertiary carnivore of this system. Evidence suggests that the giant sea bass population is recently returning to southern California waters since the mid-1990s (Pondella and Allen 2008) after close to 70 years of near extirpation. A contemporary presence of these large megacarnivores could greatly influence community dynamics as their presence since our study has boomed within southern California kelp forests.

Future research should focus on documenting continued differences inside and outside of these long-standing MPAs, as well as newly formed MPAs from the Marine Life Protection Act as of 2012, over longer periods of time throughout the Southern California Bight. This is necessary in order to further learn and provide information for fisheries management on what impacts fishing for higher trophic level species may have, not just within the fish community, but the kelp forest ecosystem off southern California.

Our study provides evidence that fishing not only directly affects targeted fishes in higher trophic levels, but also indirectly influences the trophic structure and community makeup of kelp forest fishes off southern California. The large reductions of the most ubiquitous piscivore of this system, kelp bass, released predation pressure on an abundant prey species as well as an overall increase in primary carnivore biomass outside MPAs. This result suggests a weakening of top-down control on kelp forest reefs deficient in large kelp bass off southern California.

Acknowledgments

We express our gratitude to the following people for making this research possible. Thank you to Mark Steele, Mia Adreani, and Peter Edmunds for their invaluable input, insight, and reviewing drafts of this paper. Thank you to Jennifer Smolenski and Mike Abernathy for continuous support in the field of which made this project possible. We are grateful to Juan Aguilar and the staff at the USC Wrigley Institute for Environmental Studies for field assistance and allowing the research to be conducted from Big Fisherman Cove. We thank Jack Engle and Ed Parnell for their critical advice and input to this study, and to Steve Dudgeon for his advice on statistical analyses. Many thanks to JR Clark, Nick Evensen, Edwin Leung, and Barbara Sanchez for all their assistance. This research was supported by Summer Fellowships through the USC Wrigley Marine Science Center, CSUN Thesis Support, the Nearshore Marine Research Program at CSUN, and the Department of Biology, CSUN.

Literature Cited

Aburto-Oropeza, O., B. Erisman, G.R. Galland, I. Mascareñas-Osorio, E. Sala, and E. Ezcurra. 2011. Large recovery of fish biomass in a no-take marine reserve. PLoS One, 6(8):e23601.

Allen, L. G., and T.E. Hovey. 2001. Kelp bass. Pp. 222–223 in California's Living Marine Resources: a Status Report. (W.S. Leet, C.M. Dewees, R. Klingbeil, and E.J. Larson, eds.). Calif. Dept. Fish Game Univ. Calif. Agric. Nat. Res. Publ. SG01-11.

Anderson, M.J. 2001. A new method for non-parametric multivariate analysis of variance. Austral. Ecol., 26:32–46

— and Millar, R.B. 2004. Spatial variation and effects of habitat on temperate reef fish assemblages in northeastern New Zealand. J. Exp. Mar. Biol. Ecol., 305:191–221.

—, R.N. Gorley, and K.R. Clarke. 2008. PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods. PRIMER-E.

Downloaded from http://meridian.allenpress.com/scasbulletin/article-pdf/121/1/1/3078263/i2162-4534-121-1-1.pdf by guest on 23 December 2024

Anderson, T.W. 2001. Predator responses, prey refuges, and density-dependent mortality of a marine fish. Ecology, 82(1):245-257.

Babcock, R.C., N.T. Shears, A.C. Alcala, N.S. Barrett, G.J. Edgar, K.D. Lafferty, T.R. McClanahan, and G.R. Russ. 2010. Decadal trends in marine reserves reveal differential rates of change in direct and indirect effects. PNAS, 107(43):18256-18261.

Barrett, N.S., J.E. Graham, C.D. Buxton, and M. Haddon. 2007. Changes in fish assemblages following 10 years of protection in Tasmanian marine protected areas. J. Exp. Mar. Biol. Ecol., 345(2): 141-157.

Barry, J.P., and M.J. Ehret. 1992. Diet, food preference, and algal availability for fishes and crabs on intertidal reef communities in southern California. Environ. Biol. Fish., 37(1):75-95.

Baum, J.K., and B. Worm. 2009. Cascading top-down effects of changing oceanic predator abundances. J. Animal Ecol., 78(4):699-714.

Bernstein, B.B. and N. Jung. 1979. Selective pressures and coevolution in a kelp canopy community in southern California. Ecol. Monogr., 49:335-355.

Bianchi, G., H. Gislason, K. Graham, L. Hill, X. Jin, K. Koranteng, S. Manickchand-Heileman, I. Payá, K. Sainsbury, F. Sanchez, K. Zwanenberg. 2000. Impact of fishing on size composition and diversity of demersal fish communities. ICES J. Mar. Sci., 57(3):558-571.

Blanchard, J.L., N.K. Dulvy, S. Jennings, J.R. Ellis, J.K. Pinnegar, A. Tidd, and L.T. Kell. 2005. Do climate and fishing influence size-based indicators of Celtic Sea fish community structure? ICES J. Mar. Sci., 62(3):405-411.

Blanchette, C.A., B.R. Broitman, and S.D. Gaines. 2006. Intertidal community structure and oceanographic patterns around Santa Cruz Island, CA, USA. Mar. Biol., 149(3):689-701.

Bray, R.N., and A.W. Ebeling. 1975. Food, activity, and habitat of 3 picker-type microcarnivorous fishes in kelp forests off Santa Barbara, California. U.S. Fish. Bull., 73(4):815-829.

Brock, V.E. 1954. A preliminary report on a method of estimating reef fish populations. J. Wildl. Manag., 18:297-308.

Caley, M.J. 1993. Predation, recruitment and the dynamics of communities of coral-reef fishes. Mar. Biol., 117(1):33-43.

Carr, M.H. 1991. Patterns, mechanisms, and consequences of recruitment of temperate zone reef fish. Ph.D. Dissertation. University of California, Santa Barbara, California, USA.

— and M.A. Hixon. 1995. Predation effects on early post-settlement survivorship of coral-reef fishes. MEPS, 124(1):31-42.

Caselle, J.E., A. Rassweiler, S.L. Hamilton and R.R. Warner 2015. Recovery trajectories of kelp forest animals are rapid yet spatially variable across a network of temperate marine protected areas. Sci. Rep., 5:14102.

Clarke K.R., and R.H. Green. 1988. Statistical design and analysis for a 'biological effects' study. MEPS, 46(1):213–226.

Colin, P.L., Y.J. Sadovy, M.L. Domeier. 2003. Manual for the study and conservation of reef fish spawning aggregations. Society for the Conservation of Reef Fish Aggregations, Special Publication 1, 99 pp.

Cowen, R.K. 1983. The effects of sheephead (*Semicossyphus pulcher*) predation on red sea urchin (*Strongylocentrotus franciscanus*) populations: an experimental analysis. Oecologia 58(2):249-255.

Cross, J.N., and L.G. Allen. 1993. Fishes, pp. 459-540 in Ecology of the Southern California Bight. (M.D. Dailey, D.J. Reish, and J.W. Andersons, eds.). University of California Press.

Daan, N., H. Gislason, J.G. Pope, and J.C. Rice. 2005. Changes in the North Sea fish community: evidence of indirect effects of fishing? ICES J. Mar. Sci., 62(2):177-188.

Daskalov, G.M., A.N. Grishin, S. Rodionov, and V. Mihneva. 2007. Trophic cascades triggered by overfishing reveal possible mechanisms of ecosystem regime shifts. PNAS, 104(25):10518-10523.

Davenport, A.C., and T.W. Anderson. 2007. Positive indirect effects of reef fishes on kelp performance: the importance of mesograzers. Ecology, 88(6):1548-1561.

Dayton, P.K., M.J. Tegner, P.B. Edwards, and K.L. Riser. 1998. Sliding baselines, ghosts, and reduced expectations in kelp forest communities. Ecol. Appl., 8(2):309-322.

DeMartini, E.E., A.M. Friedlander, S.A. Sandin, and E. Sala. 2008. Differences in fish-assemblage structure between fished and unfished atolls in the northern Line Islands, central Pacific. MEPS, 365:199-215.

Dever, E.P. 2004. Objective maps of near-surface flow states near Point Conception, California. J. Phys. Oceanogr., 34(2):444-461.

Doherty, P.J., and P.F. Sale. 1986. Predation on juvenile coral reef fishes: an exclusion experiment. Coral Reefs, 4(4):225-234.

Downloaded from http://meridian.allenpress.com/scasbulletin/article-pdf/121/1/1/3078263/i2162-4534-121-1-1.pdf by guest on 23 December 2024

Domeier, M.L. 2001. Giant Sea Bass. Pp. 201-211 in California's Living Marine Resources: a Status Report. (W.S. Leet, C.M. Dewees, R. Klingbeil, and E.J. Larson, eds.) California Dept. of Fish and Game.

Dulvy, N. K., N.V. Polunin, A.C. Mill, and N.A. Graham. 2004. Size structural change in lightly exploited coral reef fish communities: evidence for weak indirect effects. Can. J. Fish. Aquat. Sci., 61(3): 466-475.

Ebeling, A.W., R.J. Larson, and W.S. Alevizon. 1980a. Habitat groups and island-mainland distribution of kelp-bed fishes off Santa Barbara, California. Pp. 403-431 in The California Islands, Proceedings of a Multidisciplinary Symposium. (D.M. Powers, ed.). Santa Barabara Museum of Natural History.

—, R.J. Larson, W.S. Alevizon, and R.N. Bray. 1980b. Annual variability of reef-fish assemblages in kelp forests off Santa Barbara, California. U.S. Fish. Bull., 78:361-377.

Eisaguirre, J.H., J.M. Eisaguirre, K. Davis, P.M. Carlson, S.D. Gaines, and J.E. Caselle. 2020. Trophic redundancy and predator size class structure drive differences in kelp forest ecosystem dynamics. Ecology, 10(5):e02993.

Erisman, B.E., L.G. Allen, J.T. Claisse, D.J. Pondella II, E.F. Miller, and J.H. Murray. 2011. The illusion of plenty: hyperstability masks collapses in two recreational fisheries that target fish spawning aggregations. Can. J. Fish. Aquat. Sci., 68(10):1705-1716.

Estes, J.A., J. Terborgh, J.S. Brashares, M.E. Power, J. Berger, W.J. Bond, S.R. Carpenter, T.E. Essington, R.D. Holt, J.B.C. Jackson, R.J. Marquis, L. Oksanen, T. Oksanen, R.T. Paine, E.K. Pikitch, W.J. Ripple, S.A. Sandin, M. Scheffer, T.W. Schoener, J.B. Shurin, A.R.E. Sinclair, M.E. Soulé, R. Virtanen, D.A. Wardle. 2011. Trophic downgrading of planet earth. Science, 333(6040):301-306.

Fisher, R.A. 1924. The conditions under which the x2 measures the discrepancy between observation and hypothesis. J.R. Stat. Soc., 87:442-450

Frank, K.T., B. Petrie, J.S. Choi, and W.C. Leggett. 2005. Trophic cascades in a formerly cod-dominated ecosystem. Science, 308(5728):1621-1623.

Froeschke, J.T., L.G. Allen, and D.J. Pondella II. 2006. The fish assemblages inside and outside of a temperate marine reserve in southern California. BSCAS, 105(3):128-142.

Gingras, M.L., D.A. Ventresca, and R.H. McGonigal. 1998. In-situ videography calibrated with two parallel lasers for calculation of fish length. Calif. Fish Game., 84(1):36-39.

Graham, M.H. 2004. Effects of local deforestation on the diversity and structure of southern California giant kelp forest food webs. Ecosystems, 7(4):341-357.

Halpern, B.S. 2003. The impact of marine reserves: do reserves work and does reserve size matter? Ecol. Appl., 13(1):117-137.

Hamilton, S.L., J.E. Caselle, D.P. Malone, and M.H. Carr. 2009. Incorporating biogeography into evaluations of the Channel Islands marine reserve network. PNAS, 107(43):18272-18277.

Harms, S., and C.D. Winant. 1998. Characteristic patterns of the circulation in the Santa Barbara Channel. J. Geophys. Res. Oceans, 103(C2):3041-3065.

Hauser, L., G.J. Adcock, P.J. Smith, J.H.B. Ramírez, and G.R. Carvalho. 2002. Loss of microsatellite diversity and low effective population size in an overexploited population of New Zealand snapper (*Pagrus auratus*). PNAS, 99(18):11742-11747.

Heppell, S. A., B.X. Semmens, S.K. Archer, C.V. Pattengill-Semmens, P.G. Bush, C.M. McCoy, S.S. Heppell, and B.C. Johnson. 2012. Documenting recovery of a spawning aggregation through size frequency analysis from underwater laser calipers measurements. Biol. Cons., 155:119-127.

Hixon, M.A., and M.H. Carr. 1997. Synergistic predation, density dependence, and population regulation in marine fish. Science, 277(5328):946-949.

Hobson, E.S., and J.R. Chess. 2001. Influence of trophic relations on form and behavior among fishes and benthic invertebrates in some California marine communities. Environ. Biol. Fish., 60(4): 411-457.

Horn, M.H. 1989. Biology of marine herbivorous fishes. Oceanogr. Mar. Biol. Ann. Rev., 27:167-272.

—, and F.P. Ojeda. 1999. Herbivory. Pp. 197-222 in Intertidal fishes: Life in two worlds. (M.H. Horn, K.L.M. Marting and M. A. Chotkowski, eds.) Academic Press, 399 pp.

—, and L.A. Ferry-Graham. 2006. Feeding Mechanisms and Trophic Interactions. pp. 387-410 in The Ecology of Marine Fishes: California and Adjacent Waters. (L.G. Allen, D.J. Pondella, and M. Horn, eds.) University of California Press, 660 pp.

Jackson, J.B.C., M.X. Kirby, W.H. Berger, K.A. Bjorndal, L.W. Botsford, B.J. Bourque, R.H. Bradbury, R. Cooke, J. Erlandson, J.A. Estes, T.P. Hughes, S. Kidwell, C.B. Lange, H.S. Lenihan, J.M. Pandolfi,

Downloaded from http://meridian.allenpress.com/scasbulletin/article-pdf/121/1/1/3078263/i2162-4534-121-1-1.pdf by guest on 23 December 2024

C.H. Peterson, R.S. Steneck, M.J. Tegner, R.B. Warner. 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science, 293(5530):629-637.

Jaco, E. M., and M.A. Steele. 2020. Early indicators of MPA effects are detected by stereo-video. MEPS, 647:161-177.

Jarvis, E.T., J.M. Allen, and R.W. Smith. 2004. Comparison of recreational fish catch trends to environment–species relationships and fishery-independent data in the Southern California Bight, 1980–2000. CalCOFI Rep., 45:167–179.

Larson, R.J., and E.E. DeMartini. 1984. Abundance and vertical distribution of fishes in a cobble-bottom kelp forest off San Onofre, California. U.S. Fish. Bull., 82(1):37-53.

Lester, S.E., B.S. Halpern, K. Grorud-Colvert, J. Lubchenco, B.I. Ruttenberg, S.D. Gaines, S. Airamé, and R.R. Warner. 2009. Biological effects within no-take marine reserves: a global synthesis. MEPS, 384(2):33-46.

Love, M.S. 2011. Certainly More Than You Want to Know about the Fishes of the Pacific Coast: A Post-modern Experience. Really Big Press, 650 pp.

Mueter, F.J., and B.L. Norcross. 2000. Changes in species composition of the demersal fish community in nearshore waters of Kodiak Island, Alaska. Can. J. Fish. Aquat. Sci., 57(6):1169-1180.

Mumby, P.J., C.P. Dahlgren, A.R. Harborne, C.V. Kappel, F. Micheli, D.R. Brumbaugh, K.E. Holmes, J.M. Mendes, K. Broad, J.N. Sanchirico, K. Buch, S. Box, R.W. Stoffle, A.B. Gill. 2006. Fishing, trophic cascades, and the process of grazing on coral reefs. Science, 311(5757): 98–101.

Murdoch, W.W., S. Avery, and M.E.B. Smyth. 1975. Switching in predatory fish. Ecology, 56:1094-1105.

Myers, R.A., and B. Worm. 2003. Rapid worldwide depletion of predatory fish communities. Nature, 423(6937):280-283.

Nelson, B.V., and R.R. Vance. 1979. Diel foraging patterns of the sea urchin *Centrostephanus coronatus* as a predator avoidance strategy. Mar. Biol., 51(3):251-258.

Parnell, P.E., P.K. Dayton, C.E. Lennert-Cody, L.L. Rasmussen, and J.J. Leichter. 2006. Marine reserve design: optimal size, habitats, species affinities, diversity, and ocean microclimate. Ecol. Appl., 16(3):945-962.

Pauly, D., V. Christensen, J. Dalsgaard, R. Froese, and F. Torres. 1998. Fishing down marine food webs. Science, 279(5352):860-863.

Polis, G.A., and D.R. Strong. 1996. Food web complexity and community dynamics. Am. Nat., 147: 813-846.

Pondella D.J. II, and L.G. Allen. 2008. The decline and recovery of four predatory fishes from the Southern California Bight. Mar. Biol., 154(2):307-313.

—, S.E. Piacenza, J.T. Claisse, C.M. Williams, J.P. Williams, A.J. Zellmer, J.E. Caselle 2019. Assessing drivers of rocky reef fish biomass density from the Southern California Bight. MEPS, 628: 125-140.

Quast, J.C. 1968a. Observations on the Food and Biology of the Kelp Bass, *Paralabrax clathratus* with notes on its sportfishery at San Diego, California. pp. 81-108 in Utilization of Kelp-bed Resources in Southern California (W.J. North and C.L. Hubbs, eds.). California Department of Fish and Game, Fish Bulletin 139.

—. 1968b. Observations on the Food of the Kelp-bed Fishes. pp. 143-149 in Utilization of Kelp-bed resources in Southern California (W.J. North and C.L. Hubbs, eds.). California Department of Fish and Game, Fish Bulletin 139.

R Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria.

Schmitt, R.J., and S.J. Holbrook. 1985. Patch selection by juvenile black surfperch (Embiotocidae) under variable risk: interactive influence of food quality and structural complexity. J. Exp. Mar. Biol. Ecol., 85(3):269-285.

Shapiro, S.S., and M.B. Wilk. 1965. An analysis of variance test for normality (complete samples). Biometrika, 52(3/4):591-611.

Steele, M.A. 1997a. Population regulation by post-settlement mortality in two temperate reef fishes. Oecologia, 112(1):64-74.

—. 1997b. The relative importance of processes affecting recruitment of two temperate reef fishes. Ecology, 78(1):129-145.

—. 1999. Effects of shelter and predators on reef fishes. J. Exp. Mar. Biol. Ecol., 233(1):65-79.

—, G.E. Forrester, and G.R. Almany. 1998. Influences of predators and conspecifics on recruitment of a tropical and a temperate reef fish. MEPS, 172:115-125.

Downloaded from http://meridian.allenpress.com/scasbulletin/article-pdf/121/1/1/3078263/i2162-4534-121-1-1.pdf by guest on 23 December 2024

Steneck, R.S., J. Vavrinec, and A.V. Leland. 2004. Accelerating trophic-level dysfunction in kelp forest ecosystems of the western North Atlantic. Ecosystems, 7(4):323-332.

Stephens J.S. Jr, P.A. Morris, K. Zerba, and M.S. Love. 1984. Factors affecting fish diversity on a temperate reef: the fish assemblage of Palos Verdes Point, 1974-1981. Environ. Biol. Fishes, 11(4):259-275.

Tegner, M.J. and P.K. Dayton. 2000. Ecosystem effects of fishing in kelp forest communities. ICES J. Mar. Sci.,57(3):579-589.

Tetreault, I., and R.F. Ambrose. 2007. Temperate marine reserves enhance targeted but not untargeted fishes in multiple no-take MPAs. Ecol. Appl., 17(8):2251-2267.

Watson, D. L., E.S. Harvey, G.A. Kendrick, K. Nardi, and M.J. Anderson. 2007. Protection from fishing alters the species composition of fish assemblages in a temperate-tropical transition zone. Mar. Biol., 152(5):1197-1206.

Worm, B., and R.A. Myers. 2003. Meta-analysis of cod-shrimp interactions reveals top-down control in oceanic food webs. Ecology, 84(1):162-173.

Yates, D.C., S.I. Lonhart, S.L. Hamilton 2020. Effects of marine reserves on predator-prey interactions in central California kelp forests. MEPS, 655:139-155.

Zellmer, A.J., Claisse, J.T., Williams, C.M., and Pondella, D.J. 2018. Long-term, spatial marine harvest intensity as an indicator of human impact on shallow rocky reef ecosystems. Marine Ecology, 39:e12463.

Downloaded from http://meridian.allenpress.com/scasbulletin/article-pdf/121/1/1/3078263/i2162-4534-121-1-1.pdf by guest on 23 December 2024

Bull. Southern California Acad. Sci.
121(1), 2022, pp. 27–33
© Southern California Academy of Sciences, 2022

Spot Pattern Stability During Five Years of Growth of a Captive Giant Sea Bass, *Stereolepis gigas*

Michael C. Couffer

Grey Owl Biological Consulting, 716 Marguerite Avenue, Corona del Mar, California 92625, mikecouffer@gmail.com

Adult Giant Sea Bass (*Stereolepis gigas*) (GSB) are the largest teleosts inhabiting California's nearshore habitats. They attain a maximum total length of over 2.7 m, a weight of up to 255 kg, and an age of at least 76 years (Allen 2017; Allen and Andrews 2012; Domeier 2001). All lengths hereafter are total lengths. They range from Humboldt Bay, California to Oaxaca, Mexico, including the entire Gulf of California (Cornish 2004; Domeier 2001); 73% of the species' range occurs in Mexico (Ramirez-Valdez et al. 2021). Giant Sea Bass spend just under a month as floating eggs and planktonic larvae before settling to the bottom (Benseman and Allen 2018). After planktonic settlement, the young-of-the-year (YOY) of GSB of between 10 and 80 mm occupy habitat between 2 and 38 m in depth (Benseman and Allen 2018; Couffer and Benseman 2015; Couffer 2017). The YOY at this size range occupy wide expanses of open sand or sandy-mud away from rocks, jetties, piers, debris, and other hard structures (Benseman and Allen 2018; Benseman et al. 2019; Couffer and Benseman 2015; Couffer 2017). Benseman and Allen (2018) found that newly-settled YOY were most abundant over soft-bottomed habitat within 300 m of the heads of submarine canyons that begin close to shore. Couffer (2020) described the four centers of abundance for newly-settled YOY located by Benseman and Allen (2018) as GSB nursery sites. The known California nursery sites include Redondo Beach in Los Angeles County, Newport Pier and Big Corona del Mar State Beach in Orange County, and La Jolla Shores in San Diego County. No significant submarine canyons that closely approach sandy shorelines exist along the Pacific coast side of the Baja California Peninsula; however, potential nursery site habitat exists off the tip of the peninsula and within the Gulf of California. The topic of nursery sites within the Mexican portion of the species' range remains unexplored (Couffer 2020).

The smallest verified YOY found in a nursery site was 10 mm. However, on 11 June 2021, a school of nine fish smaller than 10 mm that appeared to have very similar body shape and behavior to newly-settled YOY was filmed by a diver in the La Jolla Shores nursery site; unfortunately, the image resolution was not high enough to conclusively identify the fish as GSB. Between 10 mm and 20 mm, YOY are black with several small white patches around the face and sides (Benseman and Allen 2018; Couffer and Benseman 2015). The white patches are too variable for long-term re-identification of individuals. Black-phase YOY have large black spiny dorsal and pelvic fins and translucent soft dorsal, pectoral, anal, and caudal fins. During the black phase, black spots do not exist on the sides. When stressed, the black background often lightens considerably but no black spots appear (Couffer 2017). From approximately 20 mm to 40 mm, their background pigmentation lightens from black through a brown phase into orange. Spiny dorsal fin pigmentation mirrors the background pigmentation seen on the sides. The large pelvic fins remain black. The black background morphs to a dark brown and as the brown lightens, faint black spots begin to appear. As the brown continues to lighten, the black spots

Downloaded from http://meridian.allenpress.com/scasbulletin/article-pdf/121/1/27/3078249/i2162-4534-121-1-27.pdf by guest on 23 December 2024

become more distinct (Couffer and Benseman 2015). The background morphs from dark brown through golden-brown to become orange.

In the orange phase, the black spots are distinct against the background and may be round, dumbbell-shaped, or square. When they are agitated, the sides and both spiny and soft dorsal fins often lighten significantly; however, regardless of the stage of agitation of the fish, the black spots remain prominent. Lightening of the background pigmentation enhances the visibility of the black spots, but can obscure some white patches. When YOY leave the nursery sites by approximately 80 mm, they still manifest the orange phase.

In 2015 the author captured and distributed several YOY among public aquaria to be raised to determine whether or not individual YOY could be identified by eye by comparing underwater photos of their spot patterns during the months when they occupy the nursery sites. Although the YOY leave these nursery sites by 80 mm in the orange phase (Couffer 2020) the spot pattern study attempted to follow the development of six fish for a year, several months longer than their time spent developing in the nursery sites. This study showed that individual YOY could be distinguished from one another by eye by comparing spot pattern photos for their first year of development (Couffer 2017).

After publication in 2017, the staff of Heal the Bay Aquarium in Santa Monica, Los Angeles County, California kept their fish to continue educating the public about GSB. This afforded the opportunity to continue the spot pattern project beyond the original one-year span by following the development of this single GSB. Photographs to record spot pattern changes were reduced to six-month intervals. After five years, this individual fish could still be recognized by eye when new photographs of its spot pattern were compared with photographs taken during its first year. Figures 1 to 10 document a gradual progression over time, and figures 11 and 12 compare years one and five directly.

After the five-year photographs and measurements were taken, the aquarium secured authorization from the California Department of Fish and Wildlife to release the fish under the author's Special Use Scientific Collecting Permit No. S-200570003-20059-001. A coded internal acoustic transmitter (Vemco Ltd. model V-16) was inserted into the fish's body cavity and the fish was released into King Harbor, Redondo Beach on 23 May 2021. Receivers detected the fish moving between points off Orange and Los Angeles counties from the day of the release through May 2022.

The four known California GSB nursery sites are separated by between five and 100 km of coastline. Due to the sedentary nature of the GSB developing in the nursery sites, no movement of YOY between even the closest nursery sites has been documented in 465 hrs of focused underwater surveys by the author or by photograph and sighting form submissions to the author by California's participating sport diving community during the past seven years. Once a fish turns from black-phase to brown-phase, its background pigment contrasts well with the black spots and the edges of the black spots are sharply defined. The sedentary nature of fish within the nursery sites that are resident for only a short time, the contrast between the fish's light background and their black spots, and the low numbers of potential matches in each nursery site allow for easy comparison of spot patterns by eye without computer assistance.

Once these long-lived fish leave the nursery sites and disperse into the general population, however, it would be extremely difficult to identify individuals by eye using underwater photos because of the extremely large number of potential matches. Furthermore, as they age, their individual spots become more diffuse and there is often little or no contrast between the spots and the background. Underwater photos do not always capture all of the spots on one side. If photos are taken when the fish is at an angle to the camera, some

Downloaded from http://meridian.allenpress.com/scasbulletin/article-pdf/121/1/27/3078249/i2162-4534-121-1-27.pdf by guest on 23 December 2024

spots are in focus but other spots closer or farther from the point of focus may be blurred or distorted. Too much flash can cause reflections that obscure spots and not enough flash may render a fish too dark. For these reasons, the spot patterns of older juvenile and adult fish are often much more difficult to compare by eye than the high-contrast spot patterns presented by brown and orange-phase YOY in the nursery sites.

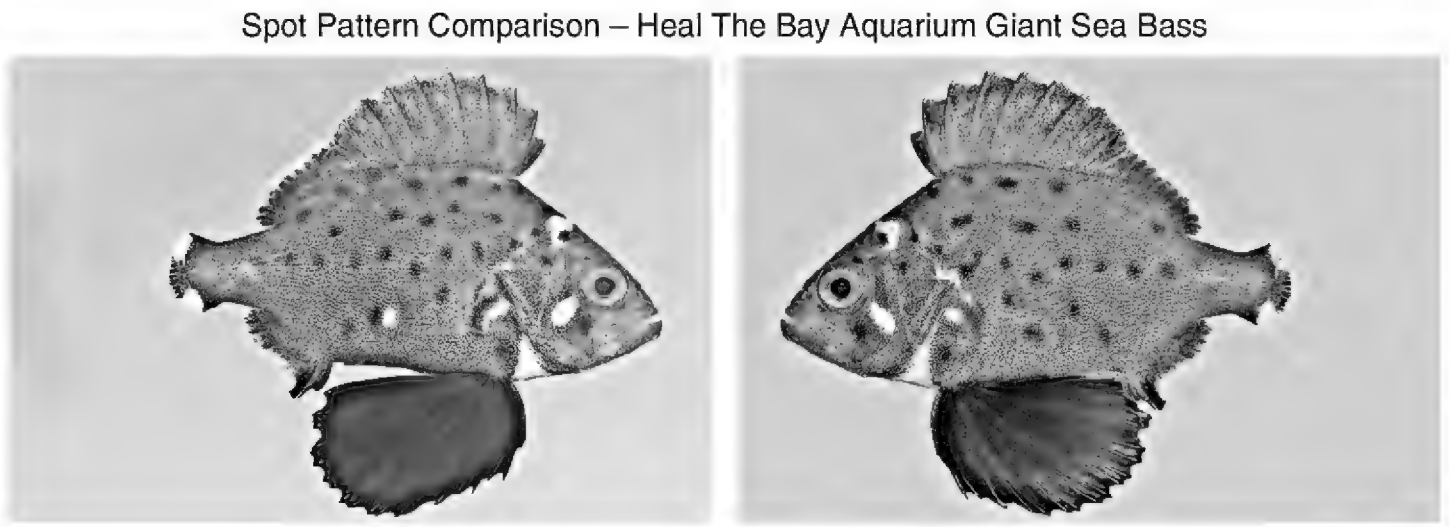


Fig. 1. Capture Date - 27 November 2015 (37.5 mm, 1.42 g).

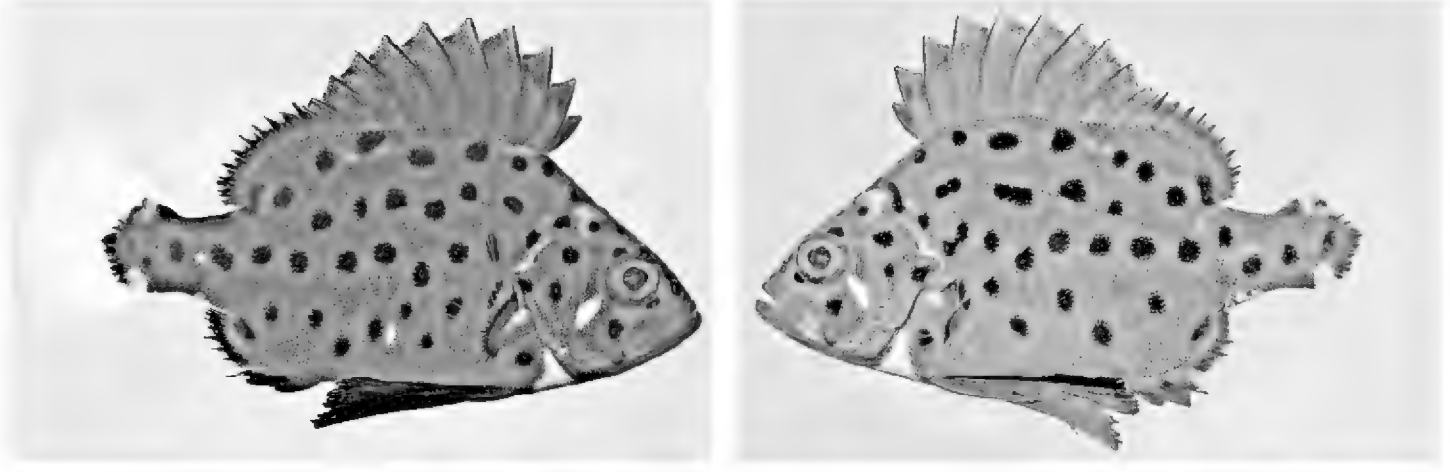


Fig. 2. 3 Months Old - 16 February 2016 (73 mm, 11 g).

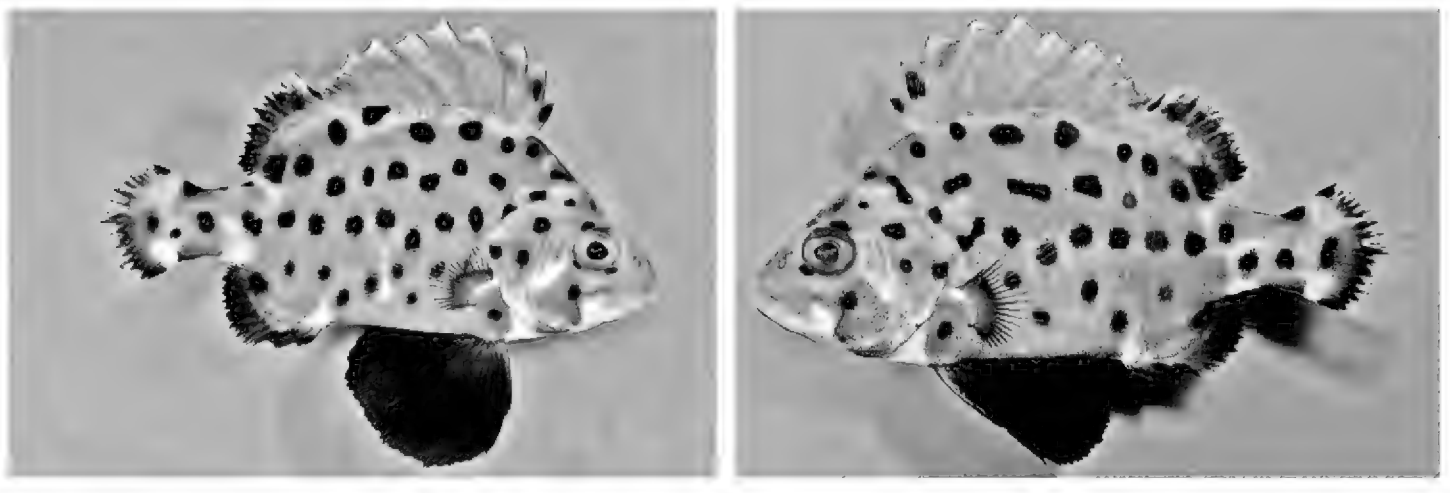


Fig. 3. 6 Months Old - 14 May 2016 (120 mm, 42 g).

Downloaded from http://meridian.allenpress.com/scasbulletin/article-pdf/121/1/27/3078249/i2162-4534-121-1-27.pdf by guest on 23 December 2024

Fig. 4. 9 Months Old - 19 August 2016 (146 mm, 67 g).

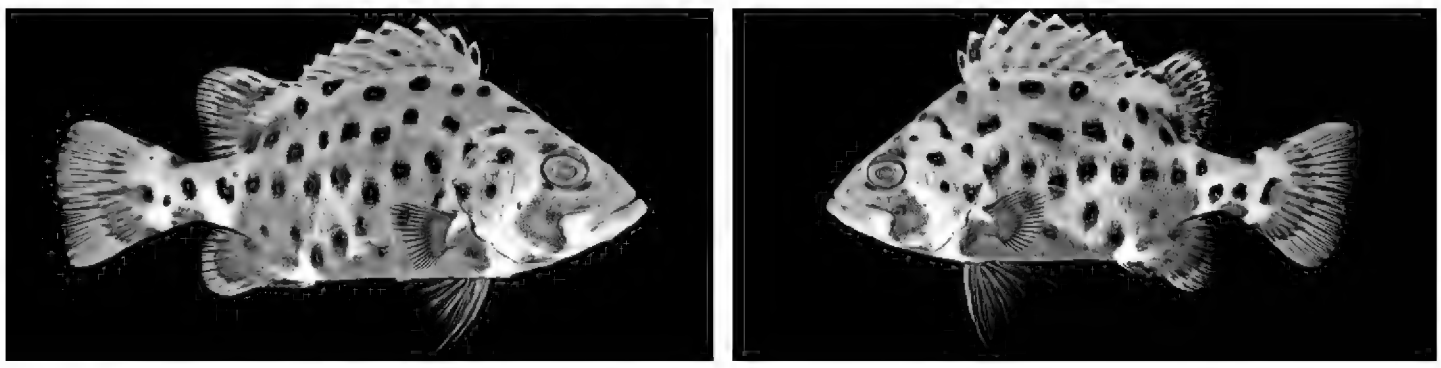


Fig. 5. 1 Year Old - 28 November 2016 (178 mm, 142 g).

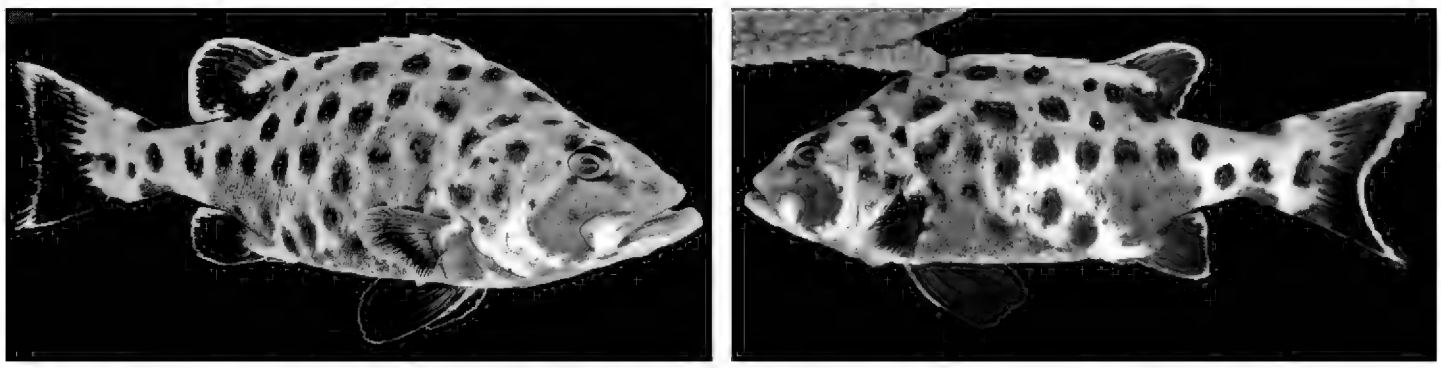


Fig. 6. 2 Years Old - 28 November 2017 (39.0 cm, 1.730 kg).

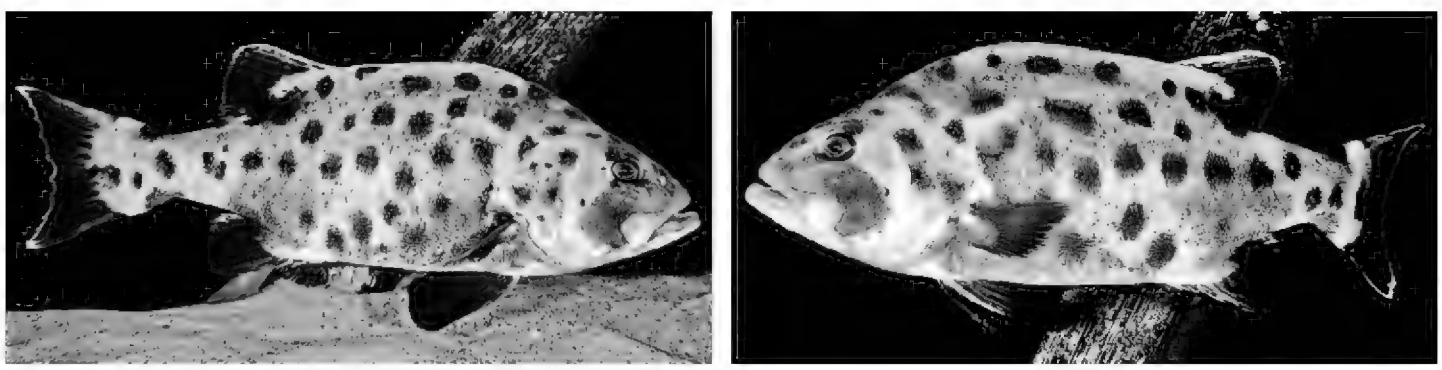


Fig. 7. 3 Years Old - 28 November 2018 (58.0 cm, 4.1 kg).

Downloaded from http://meridian.allenpress.com/scasbulletin/article-pdf/121/1/27/3078249/i2162-4534-121-1-27.pdf by guest on 23 December 2024

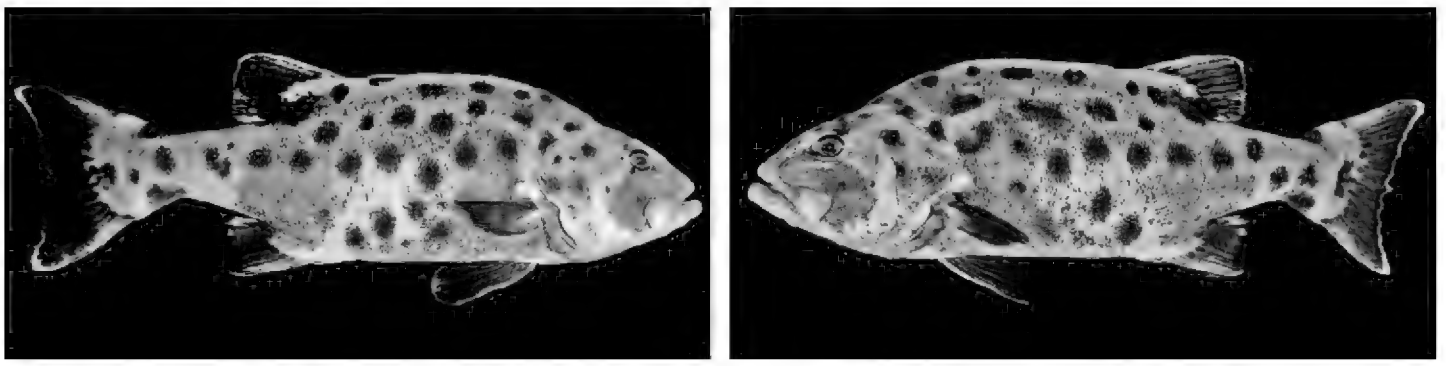


Fig. 8. 4 Years Old - 5 December 2019 (76.5 cm, 9.0 kg).

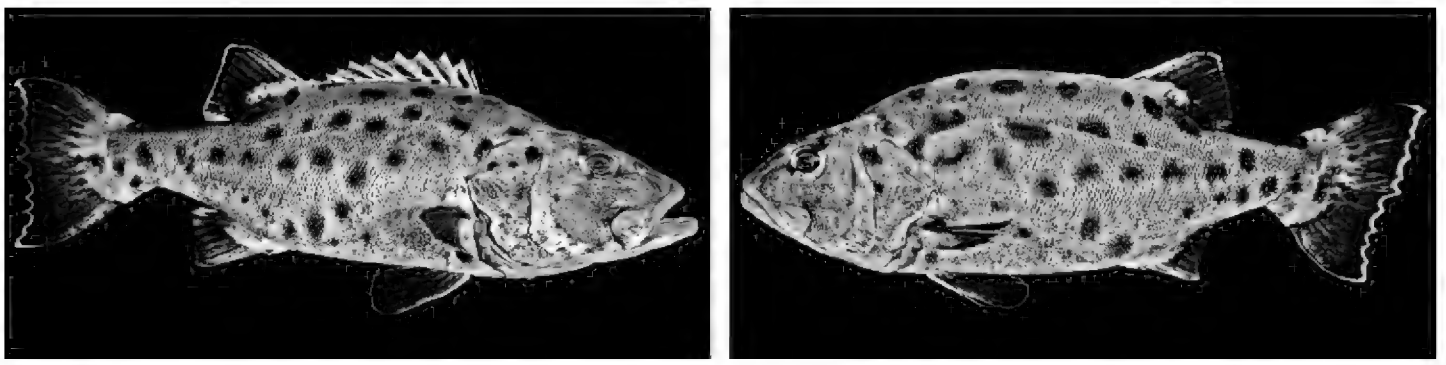


Fig. 9. 5 Years Old - 28 November 2020 (91 cm, 14.3 kg).

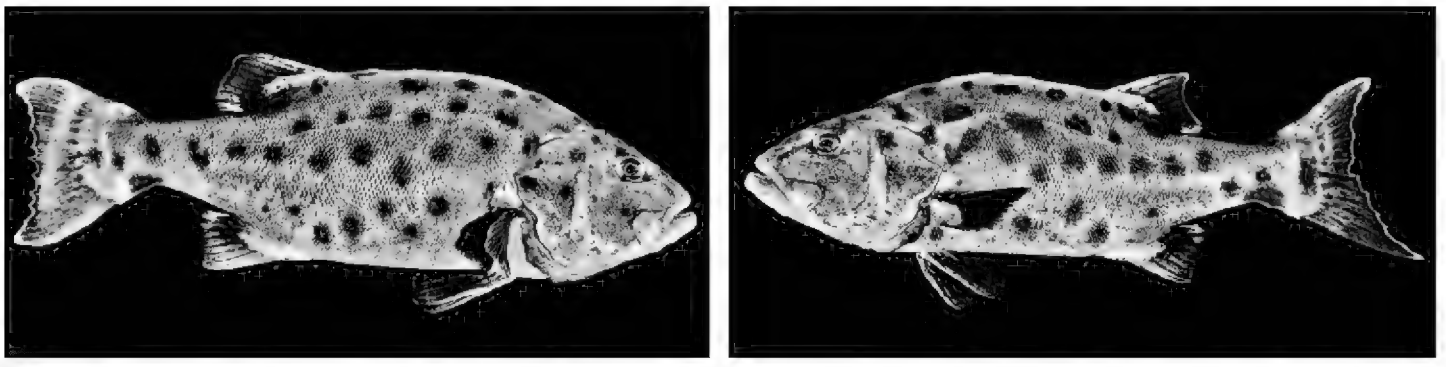


Fig. 10. 5.5 Years Old - 16 May 2021 (94 cm, 16.8 kg).

This study shows that the spot patterns can be stable enough for individual identification of GSB even after five years of growth when compared with other photos of the same fish. However, once a GSB leaves its nursery site, its spot pattern would need to be compared with all photos of fish of similar age or younger within the much larger general population so the likelihood of matching one GSB to another by eye drops precipitously. After GSB leave the nursery sites it becomes more efficient to identify and track them using pattern recognition programs coupled with databases such as a system operated at the University of California at Santa Barbara (https://spottinggiantseabass.msi.ucsb.edu) where a computer program reduces a large number of images to a few and matches are then made by eye, greatly reducing human effort needed to obtain matches (Love et al. 2018). Using this system, GSB can be matched across the species' entire geographic range for as long as the project continues. This highlights the importance of using spot pattern recognition software for GSBs outside of nursery sites, as identification of individuals by eye is only effective within the relatively closed populations of the GSB nursery sites.

Downloaded from http://meridian.allenpress.com/scasbulletin/article-pdf/121/1/27/3078249/i2162-4534-121-1-27.pdf by guest on 23 December 2024

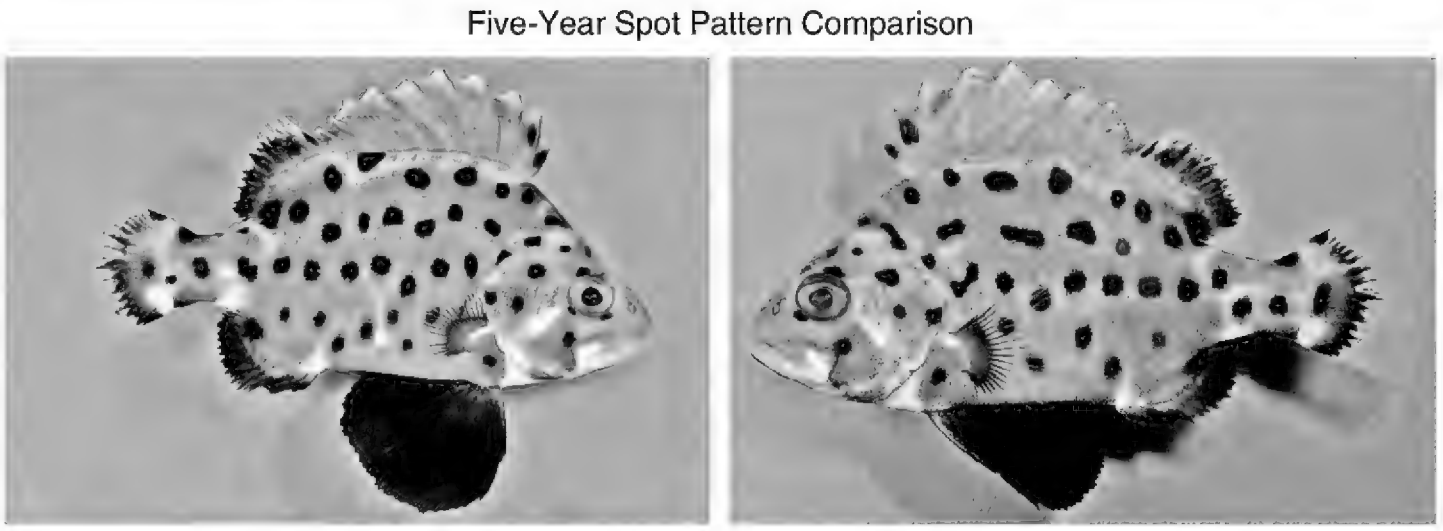


Fig. 11. 6 Months Old - 14 May 2016 (12 cm, 42 g).

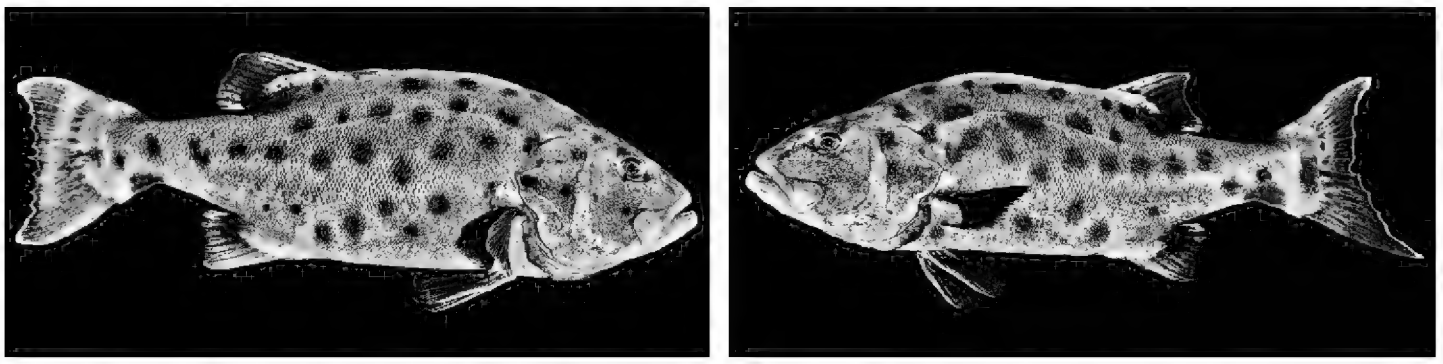


Fig. 12. 5.5 Years Old - 16 May 2021 (94 cm, 16.8 kg).

Acknowledgements

I might not have begun study of the young-of-the-year of Giant Sea Bass were it not for the insights of Master of Science candidate Stephanie A. Benseman working with her advisor Larry G. Allen of California State University at Northridge who discovered where, when, and how to find the YOY. Their preliminary work on the distribution and recruitment, and later, our observations of the behavior of YOY provided the basis to expand our understanding of the early development of this species. I would also like to thank my anonymous reviewers for providing valuable editorial comments on manuscript drafts.

Literature Cited

Allen, L.G., and A.H. Andrews. 2012. Bomb radiocarbon dating and estimated longevity of Giant Sea Bass (*Stereolepis gigas*). BSCAS, 111(1):1–14.

—. 2017. GIANTS! Or... the return of the kelp forest king. Copeia, 105(1):10–13

Benseman, S.A., and L.G. Allen. 2018. Distribution and recruitment of young of the-year Giant Sea Bass, *Stereolepis gigas*, off southern California. Copeia, 106(2):312-320.

—, M.C. Couffer and L.G. Allen. 2019. Behavior of young-of-the year of Giant Sea Bass, *Stereolepis gigas*, off the sandy beaches of Southern California. BSCAS, 118(2):79-86.

Cornish, A. (Grouper & Wrasse Specialist Group). 2004. *Stereolepis gigas*. The IUCN Red List of Threatened Species. www.iucnredlist.org

Couffer, M.C., and S.A. Benseman. 2015. A young-of-the-year Giant Sea Bass *Stereolepis gigas* buries itself in sandy bottom: a possible predator avoidance mechanism. BSCAS, 114(1):54-57.

—. 2017. Individually-unique spot patterns of young-of-the-year Giant Sea Bass, *Stereolepis gigas* in captive-raised fish. BSCAS, 116(2):98-109.

—. 2020. Planning shoreline infrastructure projects at Redondo Beach, California to avoid impacting a Giant Sea Bass nursery site. Calif. Fish Wildlife 106(1):11-18.

Downloaded from http://meridian.allenpress.com/scasbulletin/article-pdf/121/1/27/3078249/i2162-4534-121-1-27.pdf by guest on 23 December 2024

Domeier, M.L. 2001. Giant sea bass. Pp. 201-211. In California's Living Marine Resources: A Status Report. (W.S. Leet, C.M. Dewees, R. Klingbeil, and E.J. Larson, eds.). Calif. Dept. Fish Game. Sacramento, California.

Love, M.S., K. Seeto, C. Jainese, and M.M. Nishimoto. 2018. Spots on sides of Giant Sea Bass (Stereolepis gigas Ayres, 1859) are likely unique to each individual. BSCAS, 117(1):76-81.

Ramirez-Valdez, A., T.J. Rowell, K.E. Dale, M.T. Craig, L.G. Allen, J.C. Villaseñor-Derbez, A.M. Cisneros-Montemayor, A. Hernández-Velasco, J. Torre, J. Hofmeister, and B.E. Erisman. 2021. Asymmetry across international borders: Research, fishery and management trends and economic value of the giant sea bass (*Stereolepis gigas*). Fish and Fisheries, 22(6):1392-1411.

Downloaded from http://meridian.allenpress.com/scasbulletin/article-pdf/121/1/27/3078249/i2162-4534-121-1-27.pdf by guest on 23 December 2024

Bull. Southern California Acad. Sci.
121(1), 2022, pp. 34–40
© Southern California Academy of Sciences, 2022

Arboreality in the California Whipsnake (*Masticophis lateralis*): Implications for Survey Techniques

Jeff A. Alvarez[1] and Amanda C. Murphy[2]

[1] *The Wildlife Project, PO Box 188888, Sacramento, California 95818*
[2] *Wildlife Science Consulting, 627 South H Street, Livermore, California 94550*

Historically, new species were defined by mensural characters and descriptive analyses of external features (i.e., coloration, patterning, behavior) that attempted to delineate new species from those previously described. Ecological associations (e.g., habitat, microhabitat, geographic extent or location, etc.) further defined the differences between one species and those closely related (Van Denburgh 1897). Over time, the species' niche becomes better defined as various researchers use different foci or perspectives to investigate natural history traits (Storer 1925). Occasionally, natural history traits that were once considered putative, particularly in older references, are lost to the cognizance of modern researchers and become rarely referenced.

The California whipsnake [*Masticophis* (=*Coluber*) *lateralis*], first described by Hallowell in 1853, provides an example of this phenomenon. This species is a relatively long, narrow-bodied snake that is found throughout the foothills or low- to mid-elevations of portions of the Coast, Cascade, Sierra Nevada, Transverse and Peninsular Ranges in California, as well as northwestern Baja California (Stebbins 1954; Brown 1997; Grismer 2002; Flaxington 2021). Early investigators described the California whipsnake as arboreal (Grinnell and Grinnell 1907; Grinnell and Storer 1924; Ortenburger 1928; Pickwell 1947; Stebbins 1954; Appendix I), but when an extended gap in published work on snake habitat occurred, awareness of the snake's arboreal traits did not span that gap. Here, we draw upon our own recent investigations to describe arboreal traits of the California whipsnake and use those observations to suggest that it be considered semi-arboreal, and that survey and management techniques should reflect this snake's behavior. Further, we describe survey techniques designed to examine habitat features that best support the arboreal nature of this snake. Following Stebbins (1954) general natural history account, nearly 40 yrs elapsed before new information on California whipsnake habitat and microhabitat was published. Subsequent to subspeciation of *M. lateralis*, with one subspecies becoming listed as threatened in the San Francisco Bay region by state and federal wildlife agencies, a new focus on the natural history of the species was initiated (Reimer 1954; CDFW 1987; USFWS 1997, 2002). Interest in the listed Alameda whipsnake subspecies (*M. l. euryxanthus*) sparked a flurry of new observations and research beginning with Swaim and McGinnis (1992) who reported habitat associations for the Alameda whipsnake, including preferred habitat features. However, they made no mention of the arboreal behavior in the species or subspecies, nor the potential effects of this behavior on their methodology for study. Lind (1992) picked up the thread carried by early researchers when she reported that a California whipsnake was "found 2 m above ground in a canyon live oak (*Quercus chrysolepis*)..." supporting the arboreal nature of the species described in historical accounts. In 1994, Swaim prepared a detailed report on the ecology of *M. l. euryxanthus,* but arboreality and climbing ability, and its potential impact on the ground-level trapping surveys used to

Downloaded from http://meridian.allenpress.com/scasbulletin/article-pdf/121/1/34/3078245/i2162-4534-121-1-34.pdf by guest on 23 December 2024

Fig. 1. California whipsnake basking and potentially foraging in a manzanita (*Arctostphylus* sp.) shrub in Napa County, California. Photo by J.A. Alvarez.

determine presence, were not discussed. Subsequent work by Alvarez et al. (2005), Alvarez (2006), and Miller and Alvarez (2016) also focused on habitat use, but few (<2%) observations used in those analyses included specimens that were of arboreal or climbing animals. Shafer and Hein (2005) reported a detailed account of an *M. l. euryxanthus* that was feeding on an adult Lesser Goldfinch (*Carduelis pasaltria*) in a coast live oak (*Quercus agrifolia*) and included additional detail on the climbing behavior (Appendix I).

Recently, our work with *M. l. euryxanthus* has included numerous (~35) observations of arboreality (Alvarez et al. 2021). Our observations also include the species engaged in early morning basking at the top of chamise shrubs (*Adenostoma fasciculatum*), as well as closed-canopy coyote bush (*Baccharis pilularis*) stands in Contra Costa County, CA. We also noted 2 separate adult *M. lateralis* gliding (i.e., moving steadily), approximately 2 m above the ground in manzanita (*Arctostaphylos* sp.) shrubs in Napa County, CA (Fig. 1). This gliding behavior has also been reported by Pickwell (1947). During our trapping investigations we released *M. lateralis* on the ground and closely observed their movement into surrounding vegetation. Frequently these snakes sought cover as escape refuge, and immediately climbed adjacent vegetation, often 2-3 m above the ground, and then froze in a manner that made them immediately cryptic. This was in contrast to sympatric species that never attempted to climb (e.g., Pacific gopher snake [*Pituophis catenifer*], California kingsnake [*Lampropeltis californiae*], and ring-necked snake [*Diodophis punctatus*], and others) when released.

Downloaded from http://meridian.allenpress.com/scasbulletin/article-pdf/121/1/34/3078245/i2162-4534-121-1-34.pdf by guest on 23 December 2024

We noted that while climbing, *M. lateralis* regularly "reached out" with the head and up to 2/3 of the body and was able to span a distance of approximately 1 m with the body held straight vertically, horizontally, or in other postures. These observations were supported by work from Shafer and Hein (2005), who reported a *M. l. euryxanthus* extending its body straight up to move between branches. Grinnell and Storer (1924) remarked of this species, "The long slender form of the body seems to be correlative of climbing ability, as 'tree' snakes in all parts of the world are of this general form." We noted that observations of this snake's climbing behavior mimicked unrelated species we have observed in tropical habitats, like the green parrot snake (*Leptphis ahaetulla*), brown vine snake (*Oxybelis aeneus*), and brown tree snake (*Boiga irregularis*), all of which are considered fully arboreal (Rodda 1992; Savage 2002; Guyer and Donnelly 2005). California whipsnakes have similar morphological characteristics to other snakes that are considered arboreal: slender body, long length, relatively long tail (Hollowell 1853; Van Denburgh 1897, 1922; Ortenburger 1928; Grismer 2002; Stebbins 2003). Guimarães et al. (2014) suggested that body slenderness is an adaptation common among many species of arboreal snake. Pizzatto et al. (2007) also stated that body slenderness and tail length are attributes of arboreal snakes. Ortenburger (1928) reported that all members of the genus *Masticophis* have long tails (mean 27.5% of the total length), while Sheehy et al. (2016) correlated the relative length of tail with arboreality in snakes, such that snakes that are arboreal have long relative tail lengths. Guyer and Donnelly (1990) determined that arboreal snakes have a high length to mass ratio. Although we did not make any attempt to measure this in snakes we handled, we feel that the results would be self-evident, that the California whipsnake is adapted for climbing. This is not meant to imply we categorize *M. lateralis* as arboreal, but it appears clear that it is has some adaptation to arboreality and is likely a semi-arboreal snake.

Shafer and Hein (2005) reported that *M. l. euryxanthus* used the lower third of its body to grasp branches for support while climbing. Our own observations corroborate this in that we noted on several occasions that *M. lateralis* would use it's prehensile tail and posterior portion of the body to anchor itself, not only when climbing, but while grasping and swallowing prey items. The tail is, in fact, prehensile. We also noted the snake commonly moves through the habitat with its head up and away from the ground, a behavior reported by many researchers (Brown 1997; Stebbins and McGinnis 2012; Flaxington 2021). Our direct observations included two additional behaviors that indicate this species should be considered semi-arboreal. First, the head is the initial surface with which the snake perches on a branch, rocks, cliffs, or other object on to which it will eventually climb. This snake, like other well-known climbing Colubrid snakes, tilts its head at a steep angle downward at contact with the next surface above, anchoring the anterior portion of the body as it moves upward. Finally, within a tree or shrub *M. lateralis* remains relatively level while moving extremely quickly through the disjunct surfaces (Pickwell 1947).

Our experiences with this species, and those reported by numerous previous researchers, suggest that this species fills a niche that is not commonly seen in most other California snake species; a niche where known prey items, such as birds, bird eggs, and lizards, are readily available (Grinnell and Storer 1924; Grismer 2002; Flaxington 2021; Alvarez and Murphy *in Press*). Although this species can often be found foraging and basking on the ground (Hollowell 1853; Swaim and McGinnis 1992; Alvarez et al. 2005; Miller and Alvarez 2016), we feel that classifying *M. lateralis* as a semi-arboreal snake may aid in its management, particularly for the threatened subspecies. In particular, *M. l. euryxanthus* is subject to focused survey efforts that frequently declare the snake absent from areas that may be scheduled to be disturbed or developed. We suggest that habitat

Downloaded from http://meridian.allenpress.com/scasbulletin/article-pdf/121/1/34/3078245/i2162-4534-121-1-34.pdf by guest on 23 December 2024

occupancy by *M. l. euryxanthus* may often be underestimated or missed because traps are set at ground level and never in shrub or tree canopies (Swaim and McGinnis 1992; Swaim 1994, Alvarez et al. 2021). This may be due, in part, to current investigators being relatively ignorant of the habitat use (Appendix I), and/or because the species is difficult to observe in the canopy and therefore is assumed to not occur when it is actually present (Stephens 1921).

We contend that historical observations, and our own direct observations of California whipsnakes have shown that they are adapted to arboreal habitats and should be considered potentially present both on the ground and in emergent micro-habitat such as shrubs and trees. Within the range of *M. l. euryxanthus*, preconstruction surveys (i.e., visual encounter surveys) are conducted to look for snakes that may be in harm's way. This may be ineffective if that habitat is dominated by vegetation that exceeds 2 m in height (Stephens 1921). Visual encounter surveys could be improved by employing a two-step approach: cut and remove vegetation under the supervision and direction of a qualified biological monitor weeks in advance of ground disturbing activity, then conduct additional preconstruction surveys one or two days prior to ground disturbance. Alvarez et al. (2021) also suggested investigating vegetative structure, as opposed to a simple vegetation type (i.e., chaparral/scrub), when assessing potentially occupied habitat for California whipsnakes.

We note that focused academics and dedicated (i.e., permitted) researchers may in fact understand this snake's full range of behavior. However, in the last 40 years in California, the industry of biological and ecological consulting supports a much greater number of biologists than does the field of academia. The fast-paced field of consulting does not always allow for in-depth understanding of a focal species. Extensive literature reviews and field investigations are not always feasible. Our historical review of the species behavior is in support of adding methods to surveys that may allow the snake, even when uncommon in a specific location, to be detected or assumed present.

To improve detection success, surveys conducted for the threatened subspecies should consider a variety of habitat types, and testing of new survey techniques to determine ideal areas and methods for encountering snakes. This may include conducting time constrained, but lengthy visual encounter surveys of vegetation tops for basking snakes during the morning warming period (Rodda et al. 2007; timing to be tested); searching tree canopy for snakes that may have sought cover from approaching biologists, and/or testing the effectiveness of new tools such as vegetation mounted photographic devices (Siers et al. 2019). Efforts should be made to investigate the pathways by which this species crosses between large openings in and between patches of complex vegetative structure, such as habitat openings. Simultaneously, additional ground-based traplines, vegetation-based and ground-based camera traps, and visual encounter surveys should be conducted within and outside of patches of complex vegetative structure, along with inserting ground-based trap lines perpendicular to the edge of vegetative complexes. Methods should be tested that facilitate collecting snakes from within the canopy. This may include modifications to trap systems developed by Rodda et al. (1999), where traps are placed within vegetation canopies and connected by a length of rope upon which lizards or mice would have been kept for several days. The rope would replace a drift fence in ground trapping, but instead would act as a scent trail, directing snakes into traps. These and other methods should be tested to better understand how *M. lateralis* could be targeted with the intent of better understanding habitat use and developing science-based best management practices.

Downloaded from http://meridian.allenpress.com/scasbulletin/article-pdf/121/1/34/3078245/i2162-4534-121-1-34.pdf by guest on 23 December 2024

Acknowledgements

We are grateful to Jeffery T. Wilcox, of the Sonoma Mountain Ranch Preservation Foundation, who engaged in helpful discussion and reviewed a draft of the manuscript, which improved it greatly. Derek S. Jansen, of AECOM, and Emily Taylor, of California Polytechnic University, San Luis Obispo, also offered very constructive reviews that improved this manuscript greatly.

Literature Cited

Alvarez, J.A. 2006. *Masticophis lateralis euryxanthus* (Alameda whipsnake) habitat. Herpetol. Rev., 37:233.

—, K.A. Davidson, F. Villalba, D. Amador, and A.V. Sprague. 2021. Atypical habitat use by the threatened Alameda whipsnake in the eastern Bay Area of California. Western Wildlife, 8:8-12.

—, M.A, Shea, and A.C. Murphy. 2005. A compilation of observations of Alameda whipsnakes outside of typical habitat. T. W. Sec. Wil. 41:21-25.

Brown, P.R. 1997. A field guide to snakes of California. Gulf Publishing Company, viii+215 pp.

California Department of Fish and Game. 1987. Results of five-year reviews of 113 California threatened and endangered species. Non-Game Heritage Program, Sacramento, California, USA.

Flaxington, W.C. 2021. Amphibians and reptiles of California: field observations, distribution, and natural history. Fieldnotes Press, iv+294 pp.

Hallowell, E. 1853. On some new reptiles from California. PNAS, 6:236-238.

Grinnell, J., and H.W. Grinnell. 1907. Reptiles of Los Angeles County, California. Throop Polytechnic Institute, 35:1-64.

Grinnell, J., and T.I. Storer. 1924. Animal life in the Yosemite: an account of the mammals, birds, reptiles, and amphibians in a cross-section of the Sierra Nevada. University of California Press, xviii+752 pp.

Grismer, L.L. 2002. Amphibians and reptiles of Baja California, including its Pacific islands and then islands in the Sea of Cortés. University of California Press, xiii+399 pp.

Guimarães, M., M.P. Gaiarsa, and H.B. Cavalheri. 2014. Morphological adaptations to arboreal habitats and heart position in species of the neotropical whipsnakes genus *Chironius*. Acta Zool-Stockholm, 95:341-346.

Guyer, C., and M.A. Donnelly. 1990. Length-mass relationships among an assemblage of tropical snakes in Costa Rica. J. Trop. Ecol., 6:65-76.

—, and —. 2005. Amphibians and reptiles of La Selva, Costa Rica, and the Caribbean slope. University of California Press, viii+299 pp.

Lind, A.J. 1992. *Masticophis lateralis* (Striped racer). USA. California. Herpetol. Rev., 23:124.

Miller, A., and J.A. Alvarez. 2016. Habitat use and management considerations for the threatened Alameda whipsnake (*Masticophis lateralis euryxanthus*) in central California. Western Wildlife, 3:29-32.

Ortenburger, A.I. 1928. Whipsnakes and racers. Plimpton Press, Norwood, xviii+247 pp.

Pickwell, G. 1947. Amphibians and Reptiles of the Pacific States. Stanford University Press, xiv+236 pp.

Pizzatto, L., S.M. Almeida-Santos, and R. Shine. 2007. Life-history adaptations to arboreality in snakes. Ecology, 88:359-366.

Riemer, W.J. 1954. A new subspecies of the snake *Masticophis lateralis* from California. Copeia, 1954:45-58.

Rodda, G.H. 1992. Foraging behaviour of the brown tree snake, *Boiga irregularis*. Herpetol. J., 2:110-114.

—, Y. Sawai, D. Chiszar, and H. Tanaka. 1999. Problem snake management: the Habu and the brown treesnake. Comstock Publishing Associates, xix+534 pp.

—, J.A. Savidge, C.L. Tyrrell, M.T. Christy, and A.T. Ellingson. 2010. Size bias in visual searches and trapping of brown treesnakes on Guam. J. Wildlife Manag., 71:656-661.

Savage, J.M. 2002. The amphibians and reptiles of Costa Rica: A herpetofauna between two seas. University of Chicago Press, xx+934 pp.

Siers, S.R., A.B. Shiels, C.G. Payne, F.M. Chlarson, C.S. Clark, and S.M. Mosher. 2019. Photographic validation of target versus nontarget take of brown treesnake baits. Wildlife Soc. B., 43:752-759.

Shafer, C., and S. Hein. 2005. *Masticophis lateralis euryxanthus* (Alameda striped racer). Diet. Herpetol. Rev., 36:195.

Sheehy C.M. III, J.S. Albert., and H.B. Lillywhite. 2016. The evolution of tail length in snakes associated with different gravitational environments. Funct. Ecol., 30:244-254.

Downloaded from http://meridian.allenpress.com/scasbulletin/article-pdf/121/1/34/3078245/i2162-4534-121-1-34.pdf by guest on 23 December 2024

Stebbins, R.C. 1954. Amphibians and reptiles of western North America, McGraw Hill Book Company, xxii+536 pp.

—. 2003. Field guide to amphibians and reptiles of California. University of California Press, Berkeley, xiii+533 pp.

Stebbins, R.C., and S.M. McGinnis. 2012. Field guide to amphibians and reptiles of California. University of California Press, Berkeley, xiii+538 pp.

Stephens, F. 1921. Annotated list of amphibians and reptiles of San Diego County, California. T. San Diego Nat. Hist. Soc., 3:57-69.

Storer, T.I. 1925. A Synopsis of the amphibia of California. Univ. Calif. Publ. Zool., 27:1-342.

Swaim, K.E., and S.M. McGinnis. 1992. Habitat associations of the Alameda whipsnake. T. W. Sec. Wil., 28:107-111.

—. 1994. Aspects of the ecology of the Alameda whipsnake *Masticophis lateralis euryxanthus*. Thesis, California State University, Hayward, California, USA. 140 pp.

United States Fish and Wildlife Service. 1997. Endangered and threatened wildlife and plants; determination of endangered status for the Callippe silverspot butterfly and the Behren's silverspot butterfly and threatened status for the Alameda whipsnake. Federal Register 62:64306-64320.

—. 2002. Draft recovery plan for chaparral and scrub community species east of San Francisco Bay, California. Portland, Oregon, viii+173 pp.

Van Denburgh, J. 1897. The reptiles of the Pacific coast and Great Basin. Occas. P. Calif. Acad. Sci., 5:1-236.

—. 1922. The reptiles of western North America, an account of the species known to inhabit California, and Oregon, Washington, Idaho, Utah, Nevada, Arizona, British Columbia, Sonora, and lower California. Volume II snakes and turtles. Occas. P. Calif. Acad. Sci., 10:615-1028.

Downloaded from http://meridian.allenpress.com/scasbulletin/article-pdf/121/1/34/3078245/i2162-4534-121-1-34.pdf by guest on 23 December 2024

Appendix I. Quotations from historic sources regarding the climbing ability of the California whipsnake.

Author	Year	Statement (quotation)	Citation
Van Denburgh	1897	Nothing is known of the habits of this snake, except that, like other members of the genus, it is very active and a skillful climber.	Van Denburgh, J. 1897. The reptiles of the Pacific coast and Great Basin. Occas. P. Calif. Acad. Sci. 5:1-236
Grinnell and Grinnell	1907	The striped racer is a good climber and we have often seen it many feet above the ground in scrub oaks and wild lilac bushes. A curious habitat is that of lying in a rigid coil on top of a leafy branch.	Grinnell, J. and H.W. Grinnell. 1907. Reptiles of Los Angeles County, California. Throop Institute Bulletin 25:1-64.
Grinnell and Storer	1924	All the racers are rapacious snakes, and live more or less upon vertebrates; the present species, at the appropriate season, takes toll of nestling birds. The long slender form of the body seems to be correlative of climbing ability, as 'tree' snakes in all parts of the world are of this general form.	Grinnell, J., and T.I. Storer. 1924. Animal life in the Yosemite: an account of the mammals, birds, reptiles, and amphibians in a cross-section of the Sierra Nevada. University of California Press, xviii+752 pp.
Ortenburger	1928	They appear to leave the ground more frequently than red racers.	Ortenburger, A.I. 1928. Whipsnakes and racers. Plimpton Press, Norwood, xviii+247 pp.
Pickwell	1947	This racer is especially adept at climbing through the trees of the chaparral, where it may be seen gliding along at great speed three or four feet above the ground, seeming only to brush gently over the twigs and branches as it glides rapidly to the ground some fifty to sixty feet away.	Pickwell, G. 1947. Amphibians and Reptiles of the Pacific States. Stanford University Press, xiv+236 pp.
Stebbins	1954	This snake is a good climber and has been observed foraging and sunning in bushes and trees. When alarmed it may seek escape by climbing into vegetation.	Stebbins, R.C. 1954. Amphibians and reptiles of western North America, McGraw Hill Book Company, xxii+536 pp.
Shafer and Hein	2005	The snake was first observed about 5 meters above the ground in a coast live oak (*Quercus agrifolia*) with an adult lesser goldfinch (*Carduelis pasaltria*) in its mouth. After several minutes, the snake released the goldfinch onto a clump of oak leaves, repositioned itself, and began to consume the bird again. While gripping the branch with the lower third of its body, and with the bird in its mouth, the snake extended about two thirds of its body straight up to a higher branch with a grip on the lower branch as it's only support. After reaching the upper branch, it continued to climb while simultaneously swallowing the bird. The snake finished swallowing the goldfinch after 20 minutes, and was last seen on a branch about 6 meters high near the trunk of the tree.	Shafer, C., and S. Hein. 2005 *Masticophis lateralis euryxanthus* (Alameda striped racer). Diet. Herpetological Review 36:195.

Downloaded from http://meridian.allenpress.com/scasbulletin/article-pdf/121/1/34/3078245/i2162-4534-121-1-34.pdf by guest on 23 December 2024